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ALESSANDRO GARASSINO & GÜNTER SCHWEIGERT

THE UPPER JURASSIC SOLNHOFEN DECAPOD CRUSTACEAN FAUNA: REVIEW OF THE TYPES FROM OLD DESCRIPTIONS

Part I. Infraorders Astacidea, Thalassinidea, and Palinura

MILANO MAGGIO 2006

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Alessandro Garassino & Günter Schweigert

Museo Civico di Storia Naturale di Milano, Sezione di Paleontologia
Staatliches Museum für Naturkunde, Stuttgart

The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions

Part I. Infraorders Astacidea, Thalassinidea, and Palinura

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In copertina: *Cycleryon propinquus* (Schlotheim, 1822). Reconstruction F. Fogliazza.

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The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions
Part I. Infraorders Astacidea, Thalassinidea, and Palinura

To Giorgio Teruzzi
"Le seul et le vrai moyen d'avancer la science est de travailler à la description et à l'histoire des differentes choses qui en font l'objet.
Buffon.
(Discours de la manière d'étudier et de traiter l'Histoire Naturelle)

Abstract – The decapod crustacean fauna from Solnhofen and Eichstätt has not been reviewed since the studies by Schlotheim (1820, 1822), Germar (1827), v. Meyer (1836), Münster (1839), Oppel (1861, 1862), Woodward (1866), and v. Knebel (1907). Since many species were described by few or poorly preserved specimens, a review of the original sample, today housed in various German museum's collections, was necessary in order to establish their true systematic validity.

This review is divided into two parts: infraorders Astacidea Latreille, 1803, Thalassinidea Latreille, 1831, and Palinura Latreille, 1803, in the first and superfamily Penaeoidea Rafinesque-Schmaltz, 1815, plus infraorder Caridea Dana, 1852, in the second (Schweigert & Garassino, in press).

The original sample of the infraorder Astacidea Latreille, 1803, consisting of 60 specimens (originally 515), was enriched with specimens discovered in new quarries and housed in private collections to expand morphological descriptions. This review documented the systematic validity of the following species: *Eryma modestiforme* (Schlotheim, 1822), *E. veltheimii* (Münster, 1839), *Palaeastacus fuciformis* (Schlotheim, 1822), *Pustulina minuta* (Schlotheim, 1822) (family Erymidae Van Straelen, 1924); *Pseudastacus pustulosus* (Münster, 1839) (family Protastacidae Albrecht, 1983); *Stenochirus angustus* (Münster, 1839), and *S. mayeri* Oppel, 1862 (family Stenochiridae Beurlen, 1930); *Glyphea pseudoscyllarus* (Schlotheim, 1822), *G. tenuis* Oppel, 1861, *G. verrucosa* Münster, 1839, and *Squamosoglyphea squamosa* (Münster, 1839) (family Glypheidae Winckler, 1883); *Mecochirus longimanatus* (Schlotheim, 1822) (family Mecochiridae Van Straelen, 1924). At the same time, the comparative study among the species belonging to same genera resulted in the following synonymies: *Eryma leptodactylina* (Germar, 1827) = *E. modestiforme*, and *Mecochirus bajeri* Germar, 1827 = *M. longimanatus*. Moreover, we recognized that *Pseudastacus muensteri* Oppel, 1862, must be considered the female of *P. pustulosus*, and *Mecochirus brevimanus* (Münster, 1839) must be considered the female of *M. longimanatus*. The generic position of *Glyphea verrucosa* Münster, 1839, is still unclear.

The original sample of the infraorder Thalassinidea Latreille, 1831, consists of 9 specimens (originally 19). This review documented the systematic validity of the following species: *Etallonia longimana* (Münster, 1839), *Magila latimana* Münster, 1839 (family Axiidae Huxley, 1879); *Orhomalus deformis* (Oppel, 1862) (indeterminate family). At the same time, the comparative study among the species belonging to the same genera resulted in the following synonymy: *Magila robusta* Oppel, 1862 = *M. desmarestii* (Münster, 1839).

The original sample of the infraorder Palinura Latreille, 1803, consisting of 44 specimens (originally 446), was enriched with specimens discovered in new quarries and housed in private collections to expand morphological descriptions. This review documented the systematic validity of the following species: *Cycleryon propinquus* (Schlotheim, 1822), *C. orbiculatus* (Münster, 1839), *C. elongatus* (Münster, 1839), *Eryon arctiformis* (Schlotheim, 1822), and *Knebelia bilobata* (Münster, 1839) (family Eryonidae De Haan, 1841); *Palaeopentacheles roettenbacheri* (Münster, 1839) (family Polychelidae Wood-Mason, 1874); *Palinurina longipes* (Münster, 1839), and *P. tenera* Oppel, 1862 (family Palinuridae Latreille, 1802); *Cancrinos claviger* Münster, 1839 (family Cancrinidae Beurlen, 1930). At the same time, the comparative study among the species belonging to same genera resulted in the following synonymies: *Cycleryon armatus* (v. Knebel, 1907) = *C. orbiculatus* (Münster, 1839), *Knebelia schuberti* (v. Meyer, 1836) = *C. propinquus*, *Palinurina pygmea* Münster, 1839 = *P. longipes*, *Cancrinos latipes* Münster, 1839 = *C. claviger*. Moreover, *Cycleryon spinimanus* (Germar, 1827) is the female of *C. propinquus* thanks to the recent review by Schweigert (2001a), *Cycleryon subrotundus* (Münster, 1839) is probably a juvenile stage of *C. orbiculatus*, and *Eryon oppeli* Woodward, 1866, must be ascribed to *Rosenfeldia* Garassino, Teruzzi & Dalla Vecchia, 1996.

Finally, we were not able to confirm the systematic validity of *Mecochirus dubius* (Münster, 1839) as a result of the poor state of preservation of the original specimens. *Magila denticulata* must be considered *nomen dubium* because the original specimen belonging to this species is lost.

Key words: Crustacea, Decapoda, lithographic limestones, Upper Jurassic, Germany.

Zusammenfassung – Die oberjurassische Zehnfußkrebs-Fauna von Solnhofen: Neubearbeitung der Typen aus alten Beschreibungen. Teil 1. Unterordnungen Astacidea, Thalassinidea und Palinura.

Die Fauna dekapoder Crustaceen aus Solnhofen und Eichstätt ist seit den Arbeiten von Schlotheim (1820, 1822), Germar (1827), v. Meyer (1836), Münster (1839), Oppel (1861, 1862), Woodward (1866), und v. Knebel (1907) nicht mehr revidiert worden. Da viele Arten auf wenige oder schlecht erhaltene Stücke begründet sind, erschien eine Neubearbeitung der Originalstücke, die heute in verschiedenen Museumssammlungen aufbewahrt wurden, unerlässlich, um deren systematische Gültigkeit zu prüfen.

Dieses Review ist in zwei Teile gegliedert: Unterordnungen Astacidea Latreille, 1803, Thalassinidea Latreille, 1831, und Palinura Latreille, 1803, im ersten Teil und Überfamilie Penaeoidea Rafinesque-Schmaltz, 1815, sowie Unterordnung Caridea Dana, 1852 im zweiten Teil (Schweigert & Garassino, in press).

Die Original-Stichprobe der Unterordnung Astacidea Latreille, 1803, bestehend aus 60 Stücken (ursprünglich 515), wurde unter Einschluss von neu entdeckten Exemplaren aus Privatsammlungen untersucht, um die morphologischen Beschreibungen zu komplettieren.Das Review resultierte in der Feststellung der taxonomischen Gültigkeit für folgende Arten: *Eryma modestiforme* (Schlotheim, 1822), *E. veltheimii* (Münster, 1839), *Palaeastacus fuciformis* (Schlotheim, 1822), und *Pustulina minuta* (Schlotheim, 1822) (Familie Erymidae Van Straelen, 1924); *Pseudastacus pustulosus* (Münster, 1839) (Familie Protastacidae Albrecht, 1983); *Stenochirus angustus* (Münster, 1839), und *S. mayeri* Oppel, 1862 (Familie Stenochiridae Beurlen, 1930); *Glyphea pseudoscyllarus* (Schlotheim, 1822), *G. tenuis* Oppel, 1861, *G. verrucosa* Münster, 1839, und *Squamosoglyphea squamosa* (Münster, 1839) (Familie Glypheidae Winckler, 1883); *Mecochirus longimanatus* (Schlotheim, 1822) (Family Mecochiridae Van Straelen, 1924). Gleichzeitig ergaben sich aus der vergleichenden Studie die folgenden Synonymien: *Eryma leptodactylinum* (Germar, 1827) = *E. modestiforme*, und *Mecochirus bajeri* Germar, 1827 = *M. longimanatus*. Außerdem erkannten wir, dass *Pseudastacus muensteri* Oppel, 1862, als das Weibchen von *P. pustulosus* und *Mecochirus brevimanus* (Münster, 1839) als das Weibchen von *M. longimanatus* betrachtet werden muss. Die Gattungszugehörigkeit von "*Glyphea*" *verrucosa* Münster, 1839 ist noch immer unklar.

Die Original-Stichprobe der Unterordnung Thalassinidea Latreille, 1831, besteht aus 9 Stücken (ursprünglich 19). Das Review ergab die taxonomische Gültigkeit der folgenden Arten: *Etallonia longimana* (Münster, 1839), und *Magila latimana* Münster, 1839 (Familie Axiidae Huxley, 1879); *Orhomalus deformis* (Oppel, 1862) (Familie indet.). Außerdem ergab sich die folgende Synonymien: *Magila robusta* Oppel, 1862 = *M. desmarestii* (Münster, 1839).

Die Original-Stichprobe der Unterordnung Palinura Latreille, 1803, bestehend aus 44 Exemplaren (ursprünglich 446), wurde zur Vervollständigung der morphologischen Beschreibung zusammen mit neu entdeckten Stücken aus Privatsammlungen untersucht. Dabei ergab sich die taxonomische Gültigkeit der folgenden Arten: *Cycleryon propinquus* (Schlotheim, 1822), *C. orbiculatus* (Münster, 1839), *C. elongatus* (Münster, 1839), *Eryon arctiformis* (Schlotheim, 1822), und *Knebelia bilobata* (Münster, 1839) (Familie Eryonidae De Haan, 1841); *Palaeopentacheles roettenbacheri* (Münster, 1839) (Familie Polychelidae Wood-Mason, 1874); *Palinurina longipes* (Münster, 1839), und *P. tenera* Oppel, 1862 (Familie Palinuridae Latreille, 1802); *Cancrinos claviger* Münster, 1839 (Familie Cancrinidae Beurlen, 1930). Hierbei ergaben sich folgende Synonymien: *Cycleryon armatus* (v. Knebel, 1907) = *C. orbiculatus* (Münster, 1839), *Knebelia schuberti* (v. Meyer, 1836) = *C. propinquus*, *Palinurina pygmea* Münster, 1839 = *P. longipes*, *Cancrinos latipes* Münster, 1839 = *C. claviger*,. Darüber hinaus erkannten wir aufgrund der kürzlich erfolgten Neubearbeitung durch Schweigert (2001a), dass *Cycleryon spinimanus* (Germar, 1827) das Weibchen zu *C. propinquus* darstellt. *Cycleryon subrotundus* (Münster, 1839) ist vermutlich nur ein Jugendstadium von *C. orbiculatus*, und *Eryon oppeli* Woodward, 1866, muss zur Gattung *Rosenfeldia* Garassino, Teruzzi & Dalla Vecchia, 1996, gestellt werden.

Schließlich waren wir aufgrund der schlechten Erhaltung der Originalstücke nicht in der Lage, die taxonomische Gültigkeit von *Mecochirus dubius* (Münster, 1839) zu bestätigen. *Magila denticulata* muss außerdem als *nomen dubium* angesehen warden, da keine Syntypen dieser Art mehr vorhanden sind, und die ursprüngliche Beschreibung ungenügend ist.

Schlüsselwörter: Crustacea, Decapoda, Plattenkalke, Oberjura, Deutschland.

Riassunto – La fauna a crostacei decapodi del Giurassico superiore di Solnhofen: revisione degli esemplari tipo dalle descrizioni originali. Parte I. Infraordini Astacidea, Thalassinidea e Palinura.

La fauna a crostacei decapodi di Solnhofen e Eichstätt non è stata più oggetto di revisione dopo gli studi condotti da Schlotheim (1820, 1822), Germar (1827), v. Meyer (1836), Münster (1839), Oppel (1861, 1862), Woodward (1866) e v. Knebel (1907). Visto che molte specie sono state descritte sulla base di pochi esemplari o di esemplari in cattivo stato di conservazione, una revisione del campione originale, attualmente depositato presso alcuni musei tedeschi era quanto mai necessaria per stabilire la validità sistematica delle specie descritte. Questa revisione ha avuto come oggetto di studio sia i decapodi natanti che quelli reptanti.

La revisione viene divisa in due parti: gli infraordini Astacidea Latreille, 1803, Thalassinidea Latreille, 1831 e Palinura Latreille, 1803, nella prima e la superfamiglia Penaeoidea Rafinesque-Schmaltz, 1815 e l'infraordine Caridea Dana, 1852, nella seconda (Schweigert & Garassino, in stampa).

Il campione originale dell'infraordine Astacidea Latreille, 1803, formato da 60 esemplari (originariamente 515), è stato integrato con esemplari rinvenuti in nuove località e depositati presso collezioni private così da approfondire le descrizioni morfologiche. Questa revisione ha documentato la validità sistematica delle seguenti specie: *Eryma modestiforme* (Schlotheim, 1822), *E. veltheimii* (Münster, 1839), *Palaeastacus fuciformis* (Schlotheim, 1822) e *Pustulina minuta* (Schlotheim, 1822) (famiglia Erymidae Van Straelen, 1924); *Pseudastacus pustulosus* (Münster, 1839) (famiglia Protastacidae Albrecht, 1983); *Stenochirus angustus* (Münster, 1839) e *S. mayeri* Oppel, 1862 (famiglia Stenochiridae Beurlen, 1930); *Glyphea pseudoscyllarus* (Schlotheim, 1822), *G. tenuis* Oppel, 1861, *G. verrucosa* Münster, 1839 e *Squamosoglyphea squamosa* (Münster, 1839) (famiglia Glypheidae Winckler, 1883); *Mecochirus longimanatus* (Schlotheim, 1822) (famiglia Mecochiridae Van Straelen, 1924). Lo studio comparativo tra le specie appartenenti allo stesso genere ha messo in evidenza le seguenti sinonimie: *Eryma leptodactylina* (Germar, 1827) = *E. modestiforme* e *Mecochirus bajeri* Germar, 1827 = *M. longimanatus*. Inoltre, riteniamo che *Pseudastacus muensteri* Oppel, 1862, sia la femmina di *P. pustulosus* e *Mecochirus brevimanus* (Münster, 1839) sia la femmina di *M. longimanatus*. La posizione sistematica di *Glyphea verrucosa* Münster, 1839, è ancora incerta.

Il campione originale dell'infraordine Thalassinidea Latreille, 1831, si compone di 9 esemplari (originariamente 19). Questa revisione ha documentato la validità sistematica delle seguenti specie: *Etallonia longimana* (Münster, 1839) e *Magila latimana* Münster, 1839 (famiglia Axiidae Huxley, 1879); *Orhomalus deformis* (Oppel, 1862) (famiglia indeterminata). Lo studio comparativo tra le specie appartenenti allo stesso genere ha messo in evidenza la seguente sinonimia: *Magila robusta* Oppel, 1862 = *M. desmarestii* (Münster, 1839).

Il campione originale dell'infraordine Palinura Latreille, 1803, formato da 44 esemplari (originariamente 446), è stato integrato con esemplari rinvenuti in nuove località e depositati presso collezioni private così da approfondire le descrizioni morfologiche. Questa revisione ha documentato la validità sistematica delle seguenti specie: *Cycleryon propinquus* (Schlotheim, 1822), *C. orbiculatus* (Münster, 1839), *C. elongatus* (Münster, 1839), *Eryon arctiformis* (Schlotheim, 1822) e *Knebelia bilobata* (Münster, 1839) (famiglia Eryonidae De Haan, 1841); *Palaeopentacheles roettenbacheri* (Münster, 1839) (famiglia Polychelidae Wood-Mason, 1874); *Palinurina longipes* (Münster, 1839) e *P. tenera* Oppel, 1862 (famiglia Palinuridae Latreille, 1802); *Cancrinos claviger* Münster, 1839 (famiglia Cancrinidae Beurlen, 1930). Lo studio comparativo tra le specie apparteneti allo stesso genere ha messo in evidenza le seguenti sinonimie: *Cycleryon armatus* (v. Knebel, 1907) = *C. orbiculatus* (Münster, 1839), *Knebelia schuberti* (v. Meyer, 1836) = *C. propinquus*, *Palinurina pygmea* Münster, 1839 = *P. longipes*, *Cancrinos latipes* Münster, 1839 = *C. claviger*. Inoltre, riconosciamo che *Cycleryon spinimanus* (Germar, 1827) è la femmina di *C. propinquus* grazie alla recente revisione di Schweigert (2001a), che *Cycleryon subrotundus* (Münster, 1839) è un probabile stadio giovanile di *C. orbiculatus* e che *Eryon oppeli* Woodward, 1866, deve essere attribuito a *Rosenfeldia* Garassino, Teruzzi & Dalla Vecchia, 1996.

Infine, non siamo in grado di confermare la validità sistematica di *Mecochirus dubius* (Münster, 1839) a causa del cattivo stato di conservazione degli esemplari originali. *Magila denticulata* deve essere considerata *nomen dubium* in quanto l'unico esemplare originale appartenente a questa specie è andato perduto.

Parole chiave: Crustacea, Decapoda, calcare litografico, Giurassico superiore, Germania.

AGE AND SETTING OF LOCALITIES

The lithographic limestones of the Upper Jurassic in southern Germany comprise a large set of localities of different ages and settings spanning an area of several hundreds of kilometres (Fig. 1). The localities in southern Franconia are often summarised as "Solnhofen Lithographic Limestones". Many fossils both in old collections and new material from fossil traders are labelled as coming from "Solnhofen". This is very misleading and makes difficult to recognise the evolutionary trends and local differences in palaeoecology. Only a very intimate knowledge of the local lithologies permits distinguishing the exact origin of the material. Recently, however, stratigraphically well-placed material comes from several scientific excavations. Besides, there exist private collections which focus on special sites. The biostratigraphic framework of the late Kimmeridgian (Upper Jurassic) was worked out by one of the authors (Schweigert *et al.*, 1996); however knowledge of the succession of ammonite faunas from the Tithonian is still in a preliminary stage.

The oldest lithographic limestones of southern Germany, most recently discovered and dated by ammonites, occur in northern Franconia, at Wattendorf near Bamberg. They are of late Kimmeridgian age (*Pseudomutabilis* Zone). Another decapod-bearing locality, not yet precisely dated, occurs in the surroundings of Regensburg (Ebenwies). A more important fossil site nearby is that of Brunn, a papery shale of late Kimmeridgian age deposited in a very shallow lagoon surrounded by calcareous green algae meadows, coral reefs, and small islands. Somewhat younger, but still of late Kimmeridgian age is the Nusplingen Lithographic Limestone in SW Germany, which is famous for its richness in fossil sharks and decapod crustaceans. This limestone was deposited in about 100 m deep lagoon surrounded by sponge-microbial mounds and islands. In the east of Eichstätt in Franconia, several localities yielded decapod crustaceans from lithographic limestones around the Kimmeridgian/Tithonian boundary, depending on the definition of the lower boundary of the Tithonian. Excavations by the Jura-Museum (Eichstätt) in the siliceous lithographic limestones of Zandt and the more biodetritic limestones of the nearby Öchselberg yield a very diverse decapod fauna in an excellent state of preservation, among them several new taxa. Other decapod faunas similar in age to those of Zandt come from quarries in the north of Eichstätt (e.g. Blumenberg, Schernfeld, Wintershof). Many old taxa were first described from this area. The "classical" lithographic limestones of Solnhofen and Langenaltheim have an early Tithonian age, clearly younger than those of the nearby Eichstätt district. Apart from mass occurrences of planktonic crinoids (*Saccocoma*), these limestones are very poor in fossils. The vertebrate fauna and other criteria suggest a more pelagic setting. Both the sections of the Eichstätt and Solnhofen districts of micritic limestones deposited in larger shallow basins, the margins of which are poorly known, because today for economic reasons only the purest limestones in the central parts of the basins are quarried. The Solnhofen Lithographic Limestone Formation is usually overlain by a hardground or another disconformity followed by the more biodetrital and silica-rich Moernsheim Formation which also has yielded many decapod crustaceans.
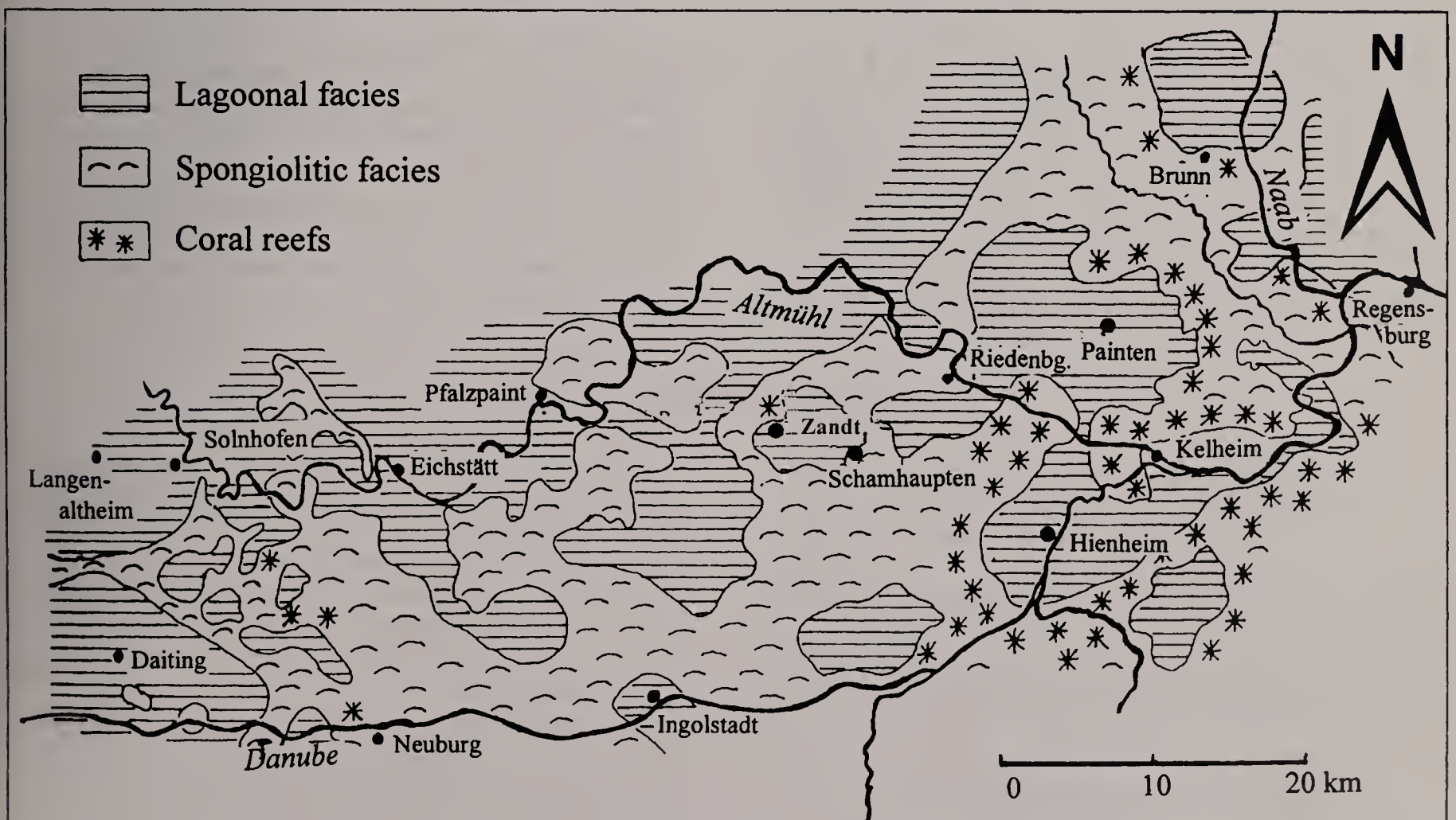
Fig. 1 – Geographic map of the fossiliferous localities.

PREVIOUS WORKS AND PRESENT STATE OF THE ART

The bulk of the decapod fauna of the lithographic limestones in southern Germany is described in monographs or short papers of the 19th century (Schlotheim, 1820, 1822; Germar, 1827; v. Meyer, 1836; Münster, 1839; Oppel, 1861, 1862; Woodward, 1866). Around the millennium, the previous discoveries of modern eryonids during deep sea expeditions encouraged the study of fossil forms (Peiser, 1904; v. Knebel, 1907). In the first half of the 20th century, both Beurlen and Glaessner, the leading authorities of fossil crustaceans in Europe, almost excluded the decapods from the lithographic limestones from their scientific works. Recently, about 56 valid taxa from Franconia and four others from the isolated locality of Nusplingen in Swabia are described. Only a few of them were briefly revised by Förster (1966, 1967, 1973, 1977). After his sudden death in 1987, the study of fossil decapods from Germany declined. From the late 1990 onwards, both scientific excavations in eastern Bavaria (Brunn), southern Franconia (Schamhaupten) and in Nusplingen (Swabia) re-stimulated the research activities of decapods (Garassino & Schweigert, 2004; Garassino *et al.*, 2005; Polz, 1999, 2000; Schweigert 2001a, 2001b, 2001c, 2002, 2003, 2004a, 2004b; Schweigert & Dietl, 1999; Schweigert & Frattigiani, 2005; Schweigert & Garassino, 2003, 2004, 2005a, 2005b, in press; Schweigert & Röper, 2001; Schweigert *et al.*, 2000, 2003). At that time it became obvious that both for palaeoenvironmental reconstruction and systematic palaeontology, it was necessary to separate the fossil material of each locality. Another strong pulse was given by the monographic documentation of "Solnhofen" fossils which were stored in various museums around the globe and in several excellent private collections (Frickhinger, 1994, 1999). Frickhinger's aim was a complete documentation of all taxa of animals and plants occurring in the "Solnhofen" limestones. From this otherwise unavailable data pool the existence of many new taxa became clear. Additionally, good material of rare or poorly preserved taxa came to light often allowing a review.

MATERIAL

This review is based on 113 specimens among the infraorders Astacidea Latreille, 1803, Thalassinidea Latreille, 1831, and Palinura Latreille, 1803. The most part of the original sample, 980 specimens, was destroyed during World War II. The survived specimens, today housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, the Geological Institute and Museum of the University of Halle, and Natur-Museum Senckenberg in Frankfurt am Main, were reviewed in order to confirm their systematic placement.

Since it was impossible to clean the original specimens of some species in order to describe some morphological characters not reported in the original descriptions, some specimens from Frattigiani, Rüdel, Tischlinger, Wulf, and Koschny private collections were used to expand the morphological descriptions of the following species: *E. modestiforme*, *P. minuta*, *P. muensteri*, *G. tenuis*, *S. angustus*, *C. elongatus*, *P. roettenbacheri*, *P. longipes*, *P. tenera*, and *M. latimana*.

One specimen in lateral view, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, was used to describe for the first time the shape of abdominal somites and the tail fan of *Cancrinos claviger*.

Finally, the total length of the specimens is taken dorsally from the tip of the rostrum to the distal extremity of the telson and the three dimensional reconstructions of the studied species reported the morphological characters observed in the original and new specimens belonging to the studied species.

The systematic palaeontology used in this paper follows the recent classification proposed by Martin & Davis (2001).

Acronyms. MNHB: Museum für Naturkunde der Humboldt-Universität (Berlin, Germany); BSPG: Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); SMF: Natur-Museum Senckenberg (Frankfurt am Main, Germany); SMNS: Staatliches Museum für Naturkunde (Stuttgart, Germany); IGH: Geological Institute and Museum of the University (Halle, Germany); BM: British Natural History Museum (London, Great Britain).

SYSTEMATIC PALAEONTOLOGY

Infraorder Astacidea Latreille, 1803
Family Erymidae Van Straelen, 1924
Genus *Eryma* v. Meyer, 1840

Type species: *Macrourites modestiformis* Schlotheim, 1822

Solnhofen species: *Eryma modestiforme* (Schlotheim, 1822); *Eryma veltheimii* (Münster, 1839)

Eryma modestiforme (Schlotheim, 1822)
Fig. 8, Pl. I (fig. 1), Pl. XI (figs. 1, 2)

1822 – *Macrourites modestiformis* Schlotheim; p. 29, Pl. 2 (fig. 3)
1822 – *Macrourites modestiformis* Schlotheim *in* Desmarest; Pl. 11 (fig. 5)
1827 – *Astacus leptodactylus* Germar; p. 100, Pl. 1 (fig. 4), **nov. syn.**
1839 – *Glyphea modestiformis* Münster; p. 19, Pl. 9 (figs. 1-3)
1839 – *Glyphea crassula* Münster; p. 17, Pl. 8 (fig. 5)
1839 – *Glyphea elongata* Münster; p. 18, Pl. 8 (fig. 8) (not figs. 11-12)
1839 – *Glyphea laevigata* Münster; p. 20, Pl. 9 (figs. 5-7)
not 1839 – *Glyphea Veltheimii* Münster; p. 22, Pl. 10 (fig. 1) = *Eryma veltheimii*, holotype
1852 – *Astacus modestiformis* Quenstedt; p. 268, Pl. 20 (fig. 15)
1855 – *Glyphea modestiformis* Münster *in* Fraas; p. 94
1857 – *Glyphea modestiformis* Münster *in* Quenstedt; p. 807, Pl. 99 (fig. 29)
not 1857 – *Glyphea Veltheimii* Münster *in* Quenstedt; p. 807, Pl. 100 (fig. 1) = *Eryma westphali* Schweigert, Dietl & Röper, 2000

1861 – *Eryma modestiformis* (Schlotheim) *in* Oppel; p. 358
1861 – *Eryma leptodactylina* (Germar) *in* Oppel; p. 358
not 1861 – *Eryma Veltheimi* Münster *in* Oppel; p. 358
not 1861 – *Eryma major* Oppel; p. 358 = *Erymastacus major*, from Nusplingen
not 1861 – *Eryma punctata* Oppel; p. 359 = *Eryma punctatum*, from Nusplingen
1862 – *Eryma modestiformis* (Schlotheim) *in* Oppel; p. 33, Pl. 6 (figs. 5-8)
1862 – *Eryma leptodactylina* (Germar) *in* Oppel; p. 35, Pl. 7 (figs. 1-4)
not 1862 – *Eryma Veltheimi* Münster *in* Oppel; p. 36, Pl. 7 (fig. 5) = *E. veltheimii*
not 1862 – *Eryma major* Oppel *in* Oppel; p. 37, Pl. 8 (fig. 3) = *Erymastacus major*
not 1862 – *Eryma punctata* Oppel *in* Oppel; p. 38, Pl. 8 (fig. 4) = *E. punctatum*
1867 – *Astacus modestiformis* Quenstedt; p. 320, Pl. 25 (fig. 15)
1885 – *Astacus modestiformis* Quenstedt; p. 409, Pl. 32 (fig. 6)
1904 – *Eryma modestiformis* (Schlotheim) *in* Walther; p. 174
1904 – *Eryma leptodactylina* (Germar) *in* Walther; p. 174
not 1904 – *Eryma Veltheimi* Münster *in* Walther; p. 174 = *E. westphali* Schweigert, Dietl & Röper, 2000
not 1908 – *Eryma veltheimi* Münster *in* Engel; p. 470 = *E. westphali* Schweigert, Dietl & Röper, 2000
1925 – *Eryma modestiformis* (Schlotheim) *in* Van Straelen; p. 272
1925 – *Eryma leptodactylina* (Germar) *in* Van Straelen; p. 273
1928 – *Eryma modestiformis* (Schlotheim) *in* Beurlen; p. 164
1928 – *Eryma pseudoventrosa* Beurlen; p. 163
not 1928 – *Eryma punctata* Oppel *in* Beurlen; p. 164 = *E. punctatum*
1928 – *Clytia leptodactylina* (Germar) *in* Beurlen; p. 170
not 1928 – *Clytia veltheimi* (Münster) *in* Beurlen; p. 170 = *E. veltheimii*
1929 – *Clytia leptodactylus* (Germar) *in* Glaessner; p. 116
1929 – *Eryma modestiformis* (Schlotheim) *in* Glaessner; p. 156
1929 – *Eryma pseudoventrosa* Beurlen *in* Glaessner; p. 158
1931 – *Eryma modestiformis* (Schlotheim) *in* Roll; p. 75
1961 – *Clytia leptodactylus* (Germar) *in* Kuhn; p. 22
1961 – *Eryma modestiformis* (Schlotheim) *in* Kuhn; p. 22
1965 – *Eryma modestiformis* (Schlotheim) *in* Förster; p. 138, Pl. 2 (fig. 5)
1966 – *Eryma modestiformis* (Schlotheim) *in* Förster; p. 118, Pl. 16 (figs. 8?-9), Pl. 17 (fig. 1)
1969 – *Eryma modestiformis* (Schlotheim) *in* Malz; p. 298, Text-fig. 7
1969 – *Eryma modestiformis* (Schlotheim) *in* Glaessner; R 455, Text-fig. 258/4
1994 – *Eryma modestiformis* (Schlotheim) *in* Frickhinger; p. 118, Text-figs. 201-202
1996 – *Eryma in* Röper, Rothgaenger & Rothgaenger; Text-fig. 90
1997 – *Eryma elongata* (Münster) *in* Dietl, Dietl, Kapitzke, Rieter, Schweigert, Ilg & Hugger; Pl. 2 (fig. 2)
1998 – *Eryma modestiformis* (Schlotheim) *in* Röper & Rothgaenger; p. 50, Text-fig. 74, Pl. 1 (fig. 86)
2000 – *Eryma modestiformis* (Schlotheim) *in* Röper, Rothgaenger & Rothgaenger; p. 91, Fig. 108
2000 – *Eryma modestiforme* (Schlotheim) *in* Schweigert, Dietl & Röper; p. 4, Text-fig. 1a, Pl. 1 (figs. 1-5)
2001 – *Eryma modestiforme* (Schlotheim) *in* Dietl & Schweigert; p. 71, Text-fig. 86
2005b – *Eryma modestiforme* (Schlotheim) *in* Schweigert & Garassino; p. 498

Diagnosis: carapace cylindrical laterally flattened; cervical groove deep and moderately inclined, not strongly sinuous and lying almost in the middle part of carapace; postcervical and branchiocardiac grooves nearly parallel and not joined; gastro-orbital groove weak; antennal and ventral grooves deep; hepatic notch and muscle adductor testis deep; rostrum short with three small supralateral teeth; antennal spine well developed; pereiopods I-III chelate; pereiopod I larger and stronger than pereiopods II-III; uropodal exopod with diaeresis.

Holotype: *Macrourites modestiformis* (= *Eryma modestiforme*), MNHB K 37 MB (Schlotheim, 1822 – Pl. 2, fig. 3; length of the specimen: 2.5 cm), housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Our studies revealed that *Astacus leptodactylus* from Solnhofen and figured by Germar (1827 – Pl. 1, fig. 4) is synonym with *Eryma modestiforme*, as discussed below. This specimen, the holotype of Germar's species, was said to be lost (Förster, 1966), but recently reappeared in the collection of the Geological Institute and Museum of the University of Halle (comm. by N. Hauschke, Halle).

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – lower Tithonian).

Type locality: Eichstätt.

Material: Oppel (1862) reported 80 specimens belonging to this species, so divided: 27 from the Redenbacher collection and 53 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample the holotype by Schlotheim, housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, and 11 additional specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified seven specimens, illustrated by Münster (1839) and two specimens, illustrated by Oppel (1862). Two specimens (BSPG AS VIII 80, AS I 623) were not illustrated by the authors. We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 191 – Münster (1839), Pl. 8 (fig. 12) – length of the specimen: 1.5 cm

BSPG AS VII 193 – Münster (1839), Pl. 8 (fig. 5) – length of the specimen: 3 cm

BSPG AS VII 194 – Münster (1839), Pl. 9 (fig. 5) – length of the specimen: 4 cm

BSPG AS VII 195 – Münster (1839), Pl. 9 (fig. 2) – length of the specimen: 3 cm

BSPG AS VII 196 – Münster (1839), Pl. 9 (fig. 3) – length of the specimen: 2 cm

BSPG AS VII 197 – Münster (1839), Pl. 9 (fig. 6) – length of the specimen: 2 cm

BSPG AS VII 198 – Münster (1839), Pl. 9 (fig. 7) – length of the specimen: 2 cm

BSPG AS VIII 81 – Oppel (1862), Pl. 6 (fig. 6) – incomplete specimen

BSPG AS VIII 82 – Oppel (1862), Pl. 6 (fig. 7) – length of the specimen: 2 cm

Oppel (1862) reported 61 specimens which he assigned to *Eryma leptodactylina* (Germar, 1827), so divided: 18 from the Redenbacher collection and 43 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. Today, we know of this original sample eight specimens, housed in Bayerische Staatssammlung für Paläontologie und Geologie in Munich, in which we identified four specimens, illustrated by Münster (1839) and four specimens, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 187 – Münster (1839), Pl. 8 (fig. 9) – length of the specimen: 4 cm

BSPG AS VII 188 – Münster (1839), Pl. 8 (fig. 8) – length of the specimen: 3 cm
BSPG AS VII 189 – Münster (1839), Pl. 9 (fig. 1) – length of the specimen: 4 cm
BSPG AS VII 190 – Münster (1839), Pl. 8 (fig. 10) – length of the specimen: 4 cm
BSPG AS VI 15 – Oppel (1862), Pl. 7 (fig. 3) – length of the specimen: 6 cm
BSPG AS VI 16 – Oppel (1862), Pl. 7 (fig. 4) – length of the specimen: 8 cm
BSPG AS VI 17 – Oppel (1862), Pl. 7 (fig. 2) – length of the specimen: 4 cm
BSPG AS VIII 79 – Oppel (1862), Pl. 7 (fig. 1) – length of the specimen: 3 cm

One specimen (n. cat. 9333 – Wulf collection) was used to describe the tail fan of this species, not preserved in the original sample.

Description. Small-sized erymid with strongly tuberculate exoskeleton.

Carapace. Carapace cylindrical, laterally flattened. Cervical groove deep, lying almost at the middle part of the carapace. Rostrum short with three small supralateral teeth directed forward. Postcervical and branchiocardiac grooves nearly parallel and not joined near their lower ends. Gastro-orbital groove deep. Antennal and ventral grooves deep. Hepatic notch and muscle adductor testis deep. Antennal spine well developed. Ocular incision large and deep. Spines short and strong located in gastric region. Pits small located in antennal, cardiac, branchial, and pterygostomial regions.

Abdomen. Somites I-V subrectangular of equal length with small pits on tergal surface. Somite VI subsquare. Pleurae of somites I-VI with pointed distal extremity. Telson subtriangular with rounded distal extremity, deep longitudinal median groove, a pair of small median spines and a pair of small spines located in the distal part of lateral margins. Protopod subrectangular. Uropodal endopod with a strong median longitudinal carina and a small spine in the distal part of outer margin. Uropodal exopod with a strong median longitudinal carina, two distal spines on the outer margin (one longer and one shorter) and rounded diaeresis with serrate upper margin having one longer median spine.

Cephalic appendages. Eyestalk short. 3rd maxilliped elongate having the first proximal article with two strong distal spines and second proximal article with one strong distal spine, all located in the lower margin. Antennular peduncles thin of which the distal one carries two elongate multiarticulate flagella of equal length. Antennal articles strong and stout of which the distal one carries a strong elongate multiarticulate flagellum, twice the body length. Scaphocerite elongate and triangular with basicerite having a strong distal spine in the lower margin.

Thoracic appendages. Pereiopod I with short and stout chela (ratio propodus/fixed finger = 1/1). Movable and fixed fingers of equal length with curved distal extremity. Inner margins of movable and fixed fingers with small rounded teeth. Surface of merus, carpus, propodus and movable finger covered with small pits and tubercles. Chela of pereiopod III longer than chela of pereiopod II. Pereiopods IV-V achelate. Pereiopod IV longer and stronger than pereiopod V. Lower margin of propodus of pereiopod IV with a row of downcurved spines.

Abdominal appendages. Pleopods with an unsegmented peduncle which carries two elongate multiarticulate flagella.

Discussion. Förster (1966) reviewed this genus, describing 35 species and pointing out that *E. modestiforme* (Schlotheim, 1822) differs from the other species of the same genus by its typical midline position of the cervical groove. Among the species described by Förster (1966), *E. verrucosa* (Münster, 1839) cannot be assigned to a genus because of the incompleteness of the lectotype (see *Pustulina minuta* in this paper). Moreover, Förster (1966) did not include among the studied species of *Eryma*, the species from the Upper Cretaceous of the United States, described by Rathbun (1923, 1926, 1935): *E. americana* Rathbun, 1923 (Black Creek Fm., N Carolina), *E. flecta* Rathbun, 1926 (Ripley Fm., Tennessee) and *E. stantoni* Rathbun, 1935 (Ripley Fm., Alabama); the species from the Upper Cretaceous (Cenomanian) of Lebanon, described by Roger (1946): *E. cretacea* Roger, 1946; the species from the Upper Jurassic (Kimmeridgian – Tithonian) of Madagascar described by Secretan (1964): *E. madagascariensis* Secretan, 1964, *E. granulifera* Secretan, 1964, and *E. australis* (Secretan, 1964).

Feldmann (1979), Garassino (1996) and Schweigert *et al.* (2000) described three new species to add to those described by the above-mentioned authors: *E. foersteri* Feldmann, 1979 (United States – Callovian), *E. meyeri* Garassino, 1996 (Italy – Sinemurian), and *E. westphali* Schweigert, Dietl & Röper, 2000 (Germany – Kimmeridgian). Finally, Crônier & Courville (2004) described *E. burgundiaca* (France – Callovian), and Feldmann & Titus (2006) described *E. jungostrix* (United States – Oxfordian).

Today, *Eryma* v. Meyer, 1840, known from the Lower Jurassic (Sinemurian) to the Upper Cretaceous (Cenomanian) of Europe (Germany, France, England, Russia and Italy), Africa (Morocco), Iran, Madagascar, Lebanon, Antarctic Peninsula, Canada, United States, and South America (Argentina), includes 47 species.

Oppel (1862), describing *E. leptodactylina* (Germar, 1827), pointed out that this species was similar to *E. modestiforme* (Schlotheim, 1822) and *E. veltheimii* (Münster, 1839), but it was different in exhibiting larger chelae on pereiopod I. However, the study of the eight original specimens by Münster and Oppel, and the very poorly preserved holotype of Germar's species allowed recognition of some morphological characters, such as the midline position of the cervical groove, rostrum with three small supralateral teeth, short and stout chela of pereiopod I not as long as described by Oppel (ratio propodus/fixed finger = 1/1, apart from the onthogenetic stage of the studied specimens) and telson with a deep median longitudinal groove and a small spine in the median part of the lateral margin. Thus, it may be useful to include *E. leptodactylina* in *E. modestiforme*. These characters distinguish *E. modestiforme* from *E. veltheimii* having a rostrum with three strong supralateral teeth and very elongate chela of pereiopod I (ratio propodus/fixed finger = 2/1) (see *E. veltheimii* in this paper).

Eryma veltheimii (Münster, 1839)
Fig. 8, Pl. I (fig. 2), Pl. XI (figs. 3, 4)

1839 – *Glyphea Veltheimii* Münster; p. 22, Pl. 10 (fig. 1)
1848 – *Eryma Veltheimi* (Münster) *in* Bronn; p. 468
1853 – *Glyphea Veltheimi* Münster *in* Frischmann; p. 28

not 1855 – *Glyphea Veltheimi* Münster *in* Fraas; p. 94 = *Eryma westphali* Schweigert, Dietl & Röper, 2000
not 1857 – *Glyphea Veltheimii* Münster *in* Quenstedt; p. 807, Pl. 100 (fig. 1) = *E. westphali* Schweigert, Dietl & Röper, 2000
1861 – *Eryma Veltheimi* (Münster) *in* Oppel; p. 358
1862 – *Eryma Veltheimi* (Münster) *in* Oppel; p. 36, Pl. 7 (fig. 5)
1996 – *Eryma in* Röper, Rothgaenger & Rothgaenger; Text-fig. 91
2000 – *Eryma veltheimi* (Münster) *in* Schweigert, Dietl & Röper; p. 7, Text-fig. 1c, Pl. 4 (figs. 1-3)
2005b – *Eryma veltheimii* (Münster) *in* Schweigert & Garassino; p. 498

Diagnosis: carapace cylindrical laterally flattened; cervical groove deep, and moderately inclined not strongly sinuous; postcervical and branchiocardiac grooves nearly parallel and joined near their lower ends; gastro-orbital groove weak; antennal and ventral grooves deep; hepatic notch and muscle adductor testis deep; rostrum short with three strong supralateral teeth; antennal spine well developed; pereiopods I-III chelate; pereiopod I larger and stronger than pereiopods II-III; uropodal exopod with diaeresis.

Holotype by monotypy: BSPG AS VII 186 a-b (Münster, 1839 – Pl. 10, fig. 1; Oppel, 1862 – Pl. 7, fig. 5), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – lower Tithonian).

Type locality: labelled as coming from Eichstätt; however, based upon the lithology of the rock matrix, the specimen comes from the Kapfelberg quarry near Kelheim (Schweigert *et al.*, 2000).

Material: Oppel (1862) reported one specimen, ascribed to this species, and housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS VII 186 a-b – Münster (1839), Pl. 10 (fig. 1) – length of the specimen: 8 cm (the specimen is preserved as part and counter-part; Münster figured the specimen with the tail fan opens in dorsal view; in realty the tail fan preserves the right uropods overlapped onto the last abdominal somites, as figured by Oppel).

BSPG AS VII 186 a-b – Oppel (1862), Pl. 7 (fig. 5)

Description. Large erymid with strongly tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened. Cervical groove deep in the anterior part of the carapace. Rostrum short with three strong supralateral teeth directed forward. Postcervical and branchiocardiac grooves nearly parallel and joined near their lower ends. Gastro-orbital groove weak. Antennal and ventral grooves deep. Hepatic notch and muscle adductor testis deep. Antennal spine well developed. Ocular incision large and deep. Spines short and strong located in gastric region. Pits small located in antennal, cardiac, branchial, and pterygostomial regions.

Abdomen. Somites I-V subrectangular of equal length with small pits on tergal surface. Somite VI subsquare. Pleurae of somites I-V with pointed distal extremity. Telson triangular with rounded distal extremity and deep median longitudinal groove. Protopod subrectangular. Uropodal endopod with a strong median longitudinal carina. Uropodal exopod with a strong longitudinal median carina, one small distal spine on the outer margin, and rounded diaeresis.

Cephalic appendages. Eyestalk short. 3rd maxilliped, antennulae and antennae not preserved.

Thoracic appendages. Pereiopod I with elongate chela (ratio propodus/fixed finger = 2/1). Movable and fixed fingers of equal length with curved distal extremity, and edentate inner margins. Upper margin of propodus with one strong distal spine. Surface of merus, carpus, propodus and movable finger covered with small pits and tubercles. Chelae of pereiopods II-III of equal length. Pereiopods IV-V achelate. Lower margin of propodus of pereiopod IV with a row of downcurved spines.

Abdominal appendages. Pleopods not preserved.

Discussion. Münster (1839) described this species on one specimen from Eichstätt. Even though incomplete, the author identified some morphological characters, such as the rostrum with three strong supralateral teeth and very elongate chelae of pereiopod I, in order to distinguish this species from *E. modestiforme* (Schlotheim, 1822). The study of the original specimen by Münster confirms the validity of these characters as diagnostic, justifying the systematic validity of *E. veltheimii* (Münster, 1839). Moreover, the presence of three characters not described by Münster, such as the joining of postcervical and branchiocardiac grooves in their lower ends, the upper margin of propodus of pereiopod I with one strong distal spine and the telson with lateral margin spineless, are useful to document the systematic validity of this species and its morphological differences from *E. modestiforme*.

Genus Palaeastacus Bell, 1850

Type species: *Astacus sussexiensis* Mantell, 1833

Palaeastacus fuciformis (Schlotheim, 1822)
Fig. 8, Pl. I (fig. 3), Pl. XI (fig. 5)

1822 – *Macrourites fuciformis* Schlotheim; p. 30, Pl. 2 (fig. 2)
1827 – *Astacus spinimanus* Germar; p. 101, Pl. 1 (fig. 3)
1829 – *Astacus fuciformis* Holl; p. 153
1839 – *Glyphea fuciformis* Münster; p. 16, Pl. 8 (figs. 1-2)
1839 – *Glyphea intermedia* Münster; p. 17, Pl. 8 (figs. 6-7)
1839 – *Glyphea crassula* Münster; p. 17, Pl. 8 (fig. 4) (not fig. 5)
1839 – *Glyphea elongata* Münster; p. 18, Pl. 8 (figs. 11-12) (not figs. 8-10)
1848 – *Eryma fuciformis* Bronn; p. 467
1852 – *Astacus fuciformis* Quenstedt; p. 268, Pl. 20 (fig. 14)
1861 – *Eryma elongata* Münster; p. 358
1861 – *Eryma fuciformis* Schlotheim; p. 359
1862 – *Eryma fuciformis* (Schlotheim) *in* Oppel; p. 41, Pl. 9 (figs. 2-6)
1862 – *Eryma elongata* Münster *in* Oppel; p. 37, Pl. 8 (figs. 1-2)
not 1862 – *Palaeastacus solitarius* Oppel; p. 46, Pl. 11 (fig. 4) = *Pustulina suevica*
1867 – *Astacus fuciformis* Quenstedt; p. 320, Pl. 25 (fig. 14)
1885 – *Astacus fuciformis* Quenstedt; p. 409, Pl. 32 (fig. 7)
1904 – *Eryma fuciformis* (Schlotheim) *in* Walther; p. 174
1925 – *Eryma elongata* Münster *in* Walther; p. 174
1925 – *Enoploclytia fuciformis* (Schlotheim) *in* Van Straelen; p. 285
not 1925 – *Palaeastacus solitarius* Oppel *in* Van Straelen; p. 289 = *P. suevica*
1928 – *Eryma fuciformis* (Schlotheim) *in* Beurlen; p. 164
1928 – *Clytia elongata* Münster *in* Beurlen; p. 170
1929 – *Clytia* sp. juv. *in* Glaessner; p. 119

1929 – *Eryma fuciformis* (Schlotheim) *in* Glaessner; p. 154
not 1929 – *Palaeastacus solitarius* Oppel *in* Glaessner; p. 290 = *P. suevica*
1961 – *Eryma fuciformis* (Schlotheim) *in* Kuhn; p. 22
not 1963 – *Glyphea fuciformis* Münster *in* Müller; p. 117, Text-fig. 157 (= *Pustulina minuta*)
1966 – *Palaeastacus fuciformis* (Schlotheim) *in* Förster; p. 130, Text-fig. 25
1968 – *Palaeastacus fuciformis* (Schlotheim) *in* Leich; p. 72
1969 – *Palaeastacus fuciformis* (Schlotheim) *in* Malz; p. 299, Text-fig. 8
not 1978 – *Eryma fuciformis* (Schlotheim) *in* Müller; Text-fig. 148a (= *P. minuta*)
1994 – *Palaeastacus fuciformis* (Schlotheim) *in* Frickhinger; p. 122, Text-figs. 218-219
2005b – *Palaeastacus fuciformis* (Schlotheim) *in* Schweigert & Garassino; p. 498

Diagnosis: carapace cylindrical laterally flattened; dorsal margin dentate; cervical and branchiocardiac grooves deep; gastro-orbital, postcervical, and ventral grooves weak; antennal groove deep; hepatic notch and muscle adductor testis weak; postcervical and branchiocardiac grooves never joined; rostrum short with three supralateral teeth; antennal spine well developed; pereiopods I-III chelate; pereiopod I larger and stronger than pereiopods II-III; uropodal exopod with diaeresis.

Holotype: *Macrourites fuciformis (= Palaeastacus fuciformis)*, MNHB K 36 MB.A. 251 (Schlotheim, 1822 – Pl. 2, fig. 2; length of the specimen: 3.5 cm), housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – lower Tithonian).

Type locality: Solnhofen (?).

Material: Oppel (1862) reported 70 specimens belonging to this species, so divided: 22 from the Redenbacher collection, three from the collection of Prof. O. Fraas in Stuttgart (SMNS, but not traceable) and 45 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample the holotype by Schlotheim, housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, and nine specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified five specimens, illustrated by Münster (1839) and four specimens, illustrated by Oppel (1862). Two specimens (BSPG AS I 620, AS VI 14 a-b) were identified as belonging to original collections thanks to the 20th century labels. However, it was impossible to establish if they were studied by one of the above-mentioned authors because the specimens were not illustrated. We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 183 – Münster (1839), Pl. 8 (fig. 2) – length of the specimen: 4.5 cm

BSPG AS VII 184 – Münster (1839), Pl. 8 (fig. 4) – length of the specimen: 3.5 cm

BSPG AS VII 185 – Münster (1839), Pl. 8 (fig. 7) – length of the specimen: 4.5 cm

BSPG AS VII 192 – Münster (1839), Pl. 8 (fig. 11) – length of the specimen: 1.5 cm

BSPG AS VI 11 – Oppel (1862), Pl. 9 (figs. 5-6) – length of the specimen: 4 cm

BSPG AS VI 12 – Oppel (1862), Pl. 9 (fig. 4) – length of the specimen: 3.5 cm

BSPG AS VI 13 – Oppel (1862), Pl. 9 (figs. 2-3) – length of the specimen: 3.5 cm

BSPG AS VI 18 – Oppel (1862), Pl. 8 (fig. 1) – length of the specimen: 1.5 cm

BSPG AS VIII 83 – Oppel (1862), Pl. 8 (fig. 2) – incomplete specimen

Description. Small-sized erymid with strongly spiny and tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened. Dorsal margin dentate. Rostrum short with three supralateral teeth. Cervical and branchiocardiac grooves deep. Gastro-orbital, postcervical, and ventral grooves weak. Antennal groove deep. Hepatic notch and muscle adductor testis weak. Antennal spine well developed. Ocular incision large and deep. Spines short and strong located in gastric, antennal, and in the upper part of branchial regions. Spines arranged in two rows in the gastric region, increasing in size toward the ocular incision. Tubercles in the pterygostomial and in the median and lower parts of branchial regions.

Abdomen. Somites I-VI subrectangular of equal length and with smooth tergal surface. Telson subtriangular with pointed distal extremity, deep median longitudinal groove, marked by two parallel rows of small spines, two oblique weak carinae and three strong spines, increasing in size from the proximal to the distal one, in the median part of lateral margins. Protopod subrectangular. Uropodal endopod with a strong median longitudinal carina. Uropodal exopod with a strong median longitudinal carina, two distal spines on the outer margin (one longer and one shorter), rounded diaeresis with serrate upper margin having one longer median spine and tuberculate lower margin.

Cephalic appendages. Eyestalk short. 3rd maxilliped elongate with first proximal article having two strong distal spines and second article with one strong distal spine, all located on the lower margin. Antennular articles thin of which the distal one carries two elongate multiarticulate flagella of equal length. Antennal articles strong and stout of which the distal one carries a strong elongate multiarticulate flagellum, twice the body length. Scaphocerite elongate and triangular with serrate lower margin and with basicerite having a strong distal spine.

Thoracic appendages. Pereiopod I with short and stout chela. Movable and fixed fingers of equal length with curved distal extremity. Fixed finger with strongly dentate inner margin. Inner margin of movable finger edentate. Upper margin of merus with a row of strong spines, increasing in length toward the articolation with carpus. Lower margin of merus with a row of strong spines of equal length. Upper margin of carpus, propodus and movable finger with a row of strong spines of equal length. Lower margin of carpus, propodus and fixed finger with a row of small spines of equal length. Surface of merus, carpus, propodus and movable finger covered with tubercles and strong spines arranged in parallel rows. Chela of pereiopod III longer than chela of pereiopod II. Chelae of pereiopods II-III with a strong spine in the articulation between movable and fixed fingers. Pereiopods IV longer and stronger than pereiopod V, both achelate. Lower margin of propodus of pereiopod IV with a row of downcurved spines.

Abdominal appendages. Pleopods with an unsegmented peduncle which carries two elongate multiarticulate flagella.

Discussion. Förster (1966) reviewed this genus, describing seven species. Today, *Palaeastacus* Bell, 1850, known from the Lower Jurassic (Sinemurian) to the Paleocene of Europe (France, Switzerland, Germany and England), Antarctic Peninsula, United States, and Australia, includes 18 species. Eight from the Jurassic: *P. falsani* (Dumortier, 1867) (France – Sinemurian), *P. argoviensis* Förster & Rieber, 1982 (Switzerland – Aalenian), *P. spinosus* (Etallon, 1861) (France – Aalenian), *P. edwardsi* Etallon, 1861 (France – Callovian), *P. fuciformis* (Schlotheim, 1822) (Germany – Tithonian), *P. rothgaengerae* Schweigert & Röper, 2001 (Germany – Kimmeridgian), *P. poeschli* Schweigert & Röper, 2001 (Germany – Tithonian), and *P. decoratus* (Frentzen, 1937) (Germany – Pliensbachian). Nine from the Cretaceous: *P. foersteri* Taylor, 1979 (Antarctic Peninsula – Aptian), *P. scaber* (Bell, 1863) (England – Albian), *P. terraereginae* (Etheridge, 1914) (Australia – Albian), *P. sussexiensis* (Mantell, 1833) (England – Cenomanian), *P. trisulcatus* Schweitzer & Feldmann, 2001 (United States – Cenomanian), *P. triglyptus* (Stenzel, 1945) (United States – Coniacian), *P. kimzeyi* Rathbun, 1935 (United States – Campanian), *P. dixoni* Bell (1850) (England – Chalk Formation), and *P. macrodactylus* Bell, 1850 (England – Chalk Formation). One from the Tertiary: *P. selmaensis* Rathbun, 1935 (United States – Paleocene).

Genus *Pustulina* Quenstedt, 1857

Type species: *Pustulina suevica* Quenstedt, 1857

Pustulina minuta (Schlotheim, 1822)
Fig. 8, Pl. II (fig. 1), Pl. XI (fig. 6), Pl. XII (figs. 1, 2)

1822 – *Macrourites minutus* Schlotheim; p. 28, Pl. 3 (fig. 3)
1839 – *Glyphea minuta* Münster; p. 20, Pl. 9 (figs. 8-10)
1839 – *Glyphea verrucosa* Münster; p. 21, Pl. 9 (fig. 11) (not fig. 12 = lectotype of *Eryma verrucosa*)
1861 – *Eryma minuta* (Schlotheim) *in* Oppel; p. 359
1862 – *Eryma minuta* (Schlotheim) *in* Oppel; p. 39, Pl. 8 (figs. 6-8)
1904 – *Eryma minuta* (Schlotheim) *in* Walther; p. 174
1925 – *Enoploclytia minuta* (Schlotheim) *in* Van Straelen; p. 284
1925 – *Enoploclytia fuciformis* (Schlotheim) *in* Van Straelen; p. 285 (pars)
1928 – *Eryma minuta* (Schlotheim) *in* Beurlen; p. 164
1929 – *Eryma fuciformis* (Schlotheim) *in* Glaessner; p. 154 (pars)
1929 – *Eryma minuta* (Schlotheim) *in* Glaessner; p. 156
1961 – *Eryma minuta* (Schlotheim) *in* Kuhn; p. 22
1966 – *Phlyctisoma minuta* (Schlotheim) *in* Förster; p. 142, Pl. 18 (fig. 9)
1969 – *Phlyctisoma minuta* (Schlotheim) *in* Malz; p. 300, Text-fig. 9
not 1994 – *Phlyctisoma minuta* (Schlotheim) *in* Frickhinger; p. 126, Fig. 224 = *Palaeastacus* sp.

Diagnosis: carapace cylindrical laterally flattened; rostrum short with three small supralateral teeth; gastro-orbital and cervical grooves deep; postcervical groove strongly developed reaching hepatic groove; branchiocardiac groove extremely small; antennal spine well developed; pereiopods I-III chelate; pereiopod I larger and stronger than pereiopods II-III; uropodal exopod with diaeresis.

Holotype: *Macrourites minutus* (= *Pustulina minuta*), MNHB K 41 MB (Schlotheim, 1822 – Pl. 3, fig. 3; length of the specimen: 2 cm), housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Our studies revealed that one the syntypes of *Glyphea verrucosa* from Eichstätt and figured by Münster (1839 – Pl. 9, fig. 11) belongs to *Pustulina minuta*, as already recognized by Oppel (1862)

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Eichstätt (?).

Material: Oppel (1862) reported 44 specimens belonging to this species, so divided: 13 from the Redenbacher collection, one from collection of the Museum für Naturkunde der Humboldt-Universität in Berlin and 30 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample the holotype by Schlotheim, housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, and four specimens, housed in Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified two specimens, illustrated by Münster (1839) and two specimens, illustrated by Oppel (1862). One specimen (BSPG AS I 619) was identified as belonging to original collections thanks to the 19th century labels. However, it was impossible to establish if it was studied by one of the above-mentioned authors because it was not illustrated. We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 180 – Münster (1839), Pl. 9 (fig. 10) – length of the specimen: 3 cm

BSPG AS VII 181 – Münster (1839), Pl. 9 (fig. 11) – length of the specimen: 3 cm

BSPG AS VI 10 – Oppel (1862), Pl. 8 (fig. 8) – length of the specimen: 3 cm

BSPG AS VIII 78 – Oppel (1862), Pl. 8 (fig. 7) – length of the specimen: 4 cm

Oppel (1862) reported one specimen, an isolated pereiopod I, which he kept in *Eryma verrucosa* (Münster, 1839), hence taking that specimen as the lectotype of this taxon. It was housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS VII 182 – Münster (1839), Pl. 9 (fig. 12)

BSPG AS VII 182 – Oppel (1862), Pl. 8 (fig. 5) – incomplete specimen

One specimen (n. cat. 0314 – Wulf collection) was used to describe the tail fan of this species, poorly preserved in the original sample.

Description. Small-sized erymid with densely tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened. Rostrum short with three small supralateral teeth. Cervical and gastro-orbital grooves deep. Postcervical groove strongly developed reaching hepatic groove. Branchiocardiac groove extremely small. Antennal, hepatic, and ventral grooves weak. Antennal spine well developed. Ocular incision small. Dorsal surface of carapace densely tuberculate.

Abdomen. Somites I-V subrectangular of equal length and with finely tuberculate tergal surface. Somite VI subsquare. Telson subtriangular with weak median longitudinal groove, two pairs of small tubercles in proximal part of dorsal surface, one pair of small distal spine on lateral margin, and rounded distal extremity. Protopod subrectangular. Uropodal endopod with strong longitudi-

nal median carina. Uropodal exopod with a weak longitudinal median carina, two different distal spines on the outer margin (one longer and one shorter) and rounded diaeresis with serrate upper margin.

Cephalic appendages. Eyestalk short. 3rd maxilliped elongate with the first article having a strong distal spine in the lower margin. Antennular articles thin of which the distal one carries two elongate multiarticulate flagella of equal length. Antennal articles strong and stout of which the distal one carries a strong elongate multiarticulate flagellum, twice the body length.

Thoracic appendages. Pereiopod I with very short and stout chela. Movable finger longer than fixed finger with curved distal extremity. Inner margins of movable and fixed fingers edentate. Surface of merus, carpus, propodus, movable, and fixed fingers covered with strong tubercles. Chelae of pereiopods II-III of equal length. Pereiopods IV-V achelate. Lower margin of propodus of pereiopod IV with a row of downcurved spines.

Abdominal appendages. Pleopods not preserved.

Discussion. *Phlyctisoma* Bell, 1863, now synonym of *Pustulina* Quenstedt, 1857, after the review by Schweigert *et al.* (2000), was studied by Förster (1966) who described seven species. Today, *Pustulina*, known from the Lower Jurassic (Sinemurian) to the Upper Cretaceous (Campanian – Maastrichtian) of Europe (Germany, England, France and Italy), Madagascar and Canada, includes 12 species. Seven from the Jurassic: *P. sinemuriana* (Garassino, 1996) (Italy – Sinemurian), *P. elegans* (Méchin, 1901) (France – Bajocian), *P. calloviensis* (Förster, 1966) (Germany – Callovian), *P. perroni* (Etallon, 1861) (France – Oxfordian), *P. pseudobabeaui* (Dollfus, 1863) (France – Kimmeridgian), *P. suevica* Quenstedt, 1857 (Germany – Kimmeridgian), and *P. minuta* (Schlotheim, 1822) (Germany – Tithonian). Five from the Cretaceous: *P. spinulata* (Secretan, 1964) (Madagascar – Valanginian-Hauterivian), *P. tuberculata* (Bell, 1863) (England – Albian), *P. granulata* (Bell, 1863) (England – Albian), *P. scabra* (Bell, 1863) (England – Albian), and *P. dawsoni* (Woodward, 1900) (Canada – Upper Cretaceous).

Münster (1839) described *Glyphea verrucosa* on one poorly preserved specimen (figured in Pl. 9, fig. 11) and one isolated complete chela. Only the latter was kept in this species by Oppel (1862), so that this chela has become the lectotype of *Glyphea verrucosa* Münster, 1839. Förster (1966) discussed the systematic position of *E. verrucosa* (Münster, 1839), rejecting the ascription of this species to *Pustulina minuta* (Schlotheim, 1822), for the different ornamentation of the chela. Moreover, the author, comparing *E. verrucosa* with *E. boloniensis* Sauvage, 1891 (France – Kimmeridgian) and *E. mosquensis* Lahusen, 1894 (Russia – Portlandian), both preserved as incomplete chelae, pointed out the existence of a morphological affinity between the propodus of the German species and the other two. However, the latter view was based on a large chela in the collection of the Naturkundemuseum in Dresden which Förster (1966) assigned to the same species. The latter, unfigured specimen of which a plaster cast exists in the Munich collection, clearly belongs to *Erymastacus* sp. in respect of its very large fingers showing occludent margins with well-developed, regularily spaced teeth. The lectotype of *Glyphea verrucosa* Münster, 1839, differs from *Pustulina minuta* by the presence of a densely pustulate ornamentation of the propodus and its more straight fingers. To date no other specimen of this rare taxon could be identified in collections, so that the generic assignment is uncertain.

Family Protastacidae Albrecht, 1983
Genus *Pseudastacus* Oppel, 1861

Type species: *Bolina pustulosa* Münster, 1839

Pseudastacus pustulosus (Münster, 1839) (♂)
Fig. 8, Pl. II (fig. 2), Pl. XII (figs. 3, 4)

1839 – *Bolina pustulosa* Münster; p. 23, Pl. 9 (fig. 13)
1840 – *Alvis octopus* Münster; p. 20, Pl. 1 (fig. 1)
1861 – *Pseudastacus pustulosus* (Münster) *in* Oppel; p. 360
1861 – *Pseudastacus Münsteri* Oppel; p. 360, **nov. syn.** (♀)
1862 – *Pseudastacus pustulosus* (Münster) *in* Oppel; p. 44, Pl. 10 (figs. 4-5), Pl. 11 (fig. 1)
1862 – *Pseudastacus Münsteri* Oppel; p. 45, Pl. 11 (fig. 2)
1904 – *Pseudastacus pustulosus* (Münster) *in* Walther; p. 174
1904 – *Pseudastacus Münsteri* Oppel *in* Walther; p. 174
1925 – *Pseudastacus pustulosus* (Münster) *in* Van Straelen; p. 292, Text-fig. 133
1929 – *Pseudastacus pustulosus* (Münster) *in* Glaessner; p. 351
1969 – *Pseudastacus pustulosus* (Münster) *in* Glaessner; R 460, Text-fig. 267/1
1994 – *Pseudastacus pustulosus* (Münster) *in* Frickhinger; p. 26, Fig. 225

Diagnosis: carapace cylindrical laterally flattened; cervical, gastro-orbital, antennal, and hepatic grooves deep; postcervical groove weak; branchiocardiac groove absent; dorsal suture absent; rostrum long with three strong supralateral teeth; antennal spine weak; pereiopods I-III chelate; pereiopod I larger and stronger than pereiopods II-III; uropodal exopod with diaeresis.

Lectotype: BSPG AS I 670 (Oppel, 1862 – Pl. 10, fig. 4), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Our studies revealed that *Pseudastacus muensteri* from Solnhofen and figured by Oppel (1862 – Pl. 11, fig. 2 a-b) is synonym with *Pseudastacus pustulosus*, as discussed below. This specimen, BSPG AS I 672, is the holotype of Oppel's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported ten specimens belonging to this species, so divided: one from the Redenbacher collection and nine from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample four specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified one specimen, illustrated by Münster (1839) and three specimens, illustrated by Oppel (1862). Seven specimens were identified as belonging to original collections thanks to the 19th century labels; two to Münster collection, four to Oppel collection and one unidentified. Finally, the specimen BSPG AS VII 323, belonging to Münster's collection was not illustrated by the author. We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 321 – Münster (1839), Pl. 9 (fig. 13) – length of the specimen: 6 cm

BSPG AS I 669 – Oppel (1862), Pl. 10 (fig. 5) – length of the specimen: 6 cm

BSPG AS I 670 – Oppel (1862), Pl. 10 (fig. 4) – length of the specimen: 6 cm

BSPG AS I 671 – Oppel (1862), Pl. 11 (fig. 1) – length of the specimen: 6 cm

Oppel (1862) reported one specimen which he assigned to *Pseudastacus muensteri* Oppel, 1862, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS I 672 – Oppel (1862), Pl. 11 (fig. 2 a-b) – length of the specimen: 4 cm

One well-preserved specimen (n. cat. SMNS 65480 – Koschny collection) was used to describe some morphological characters of the carapace, poorly preserved in the original specimens.

Description. Median-sized protoastacid with strongly tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened. Dorsal margin straight. Dorsal suture absent. Rostrum long with three strong supralateral teeth. Cervical, gastro-orbital, antennal, and hepatic grooves deep. Postcervical groove weak. Branchiocardiac groove absent. Antennal spine weak. Ocular incision large and deep.

Abdomen. Somites I-VI subrectangular of equal length with slightly tuberculate tergal surface. Telson subrectangular with rounded distal extremity and one strong distal spine on the lateral margin. A kind of transverse fold breaks telson into two almost identical parts: rigid and tuberculate upper part and flexible lower part. Protopod subrectangular. Uropodal endopod with a strong longitudinal median carina. Uropodal exopod with a strong longitudinal median carina, strong distal spine on the outer margin, and rounded diaeresis with serrate upper margin.

Cephalic appendages. Eyestalk short. 3rd maxilliped elongate and spineless. Antennular articles thin of which the distal one carries two elongate multiarticulate flagella of equal length. Antennal articles strong and elongate of which the distal one carries a strong elongate multiarticulate flagellum, twice the body length. Scaphocerite strong, elongate, and triangular with pointed distal extremity.

Thoracic appendages. Pereiopod I with short and stout chela. Movable and fixed fingers of equal length with curved distal extremity. Serrate inner margins of movable and fixed fingers. Lower margin of propodus with a row of small spines. Dorsal surface of merus with a longitudinal median row of strong tubercles. Lower margins of carpus and merus with small spines. Strong median spine on articulate margins of merus and carpus. Surface of merus, carpus, propodus, and movable finger covered with small tubercles. Chela of pereiopod II smaller than chela of pereiopod III. Pereiopods IV-V achelate.

Abdominal appendages. Pleopods with an unsegmented peduncle which carries two elongate multiarticulate flagella.

Discussion. *Pseudastacus* Oppel, 1861, was included for long time in the family Nephropidae Dana, 1852, as reported by Glaessner (1969) and Chong & Förster (1976). Albrecht (1983) reviewed this genus, including it in the new family Protastacidae Albrecht, 1983 (infraorder Astacidea Latreille, 1802). The author justified the institution of this family because it represents a transitional grade between the erymids and crayfishes. Tshudy & Babcock (1997) included *Pseudastacus* in their newly erected family Chilenophoberidae, but their analysis is not founded by a morphological review of the type material but only by line drawings in literature.

Today, the family Protastacidae includes two genera: *Pseudastacus* Oppel, 1861, with two species, *P. pustulosus* Münster, 1839, and *P. minor* Fraas, 1878 (Germany – Tithonian), and *Protoastacus* Albrecht, 1983, with *P. politus* (Schlüter, 1868) (Germany – Upper Cretaceous). The holotype of *P. dubertreti* Roger, 1946 (n. cat. B. 18892) (Lebanon – Cenomanian) housed in the Muséum national d'Histoire naturelle in Paris, was recently examined by one of the authors (A. Garassino). Its study has pointed out that the elongate rostrum with a row of dorsal teeth and the annulated carpus of pereiopods II-III are two characters typical of *Carpopenaeus callirostris* Glaessner, 1945. So *P. dubertreti* must be considered as synonym with *C. callirostris*.

Oppel (1862), describing *P. muensteri*, pointed out that the small size of the body and the longer and slender pereiopod I distinguished this new species from *P. pustulosus* (Münster, 1839). Apart from this very significant character, the specimen belonging to *P. muensteri* exhibits the same morphological characters of the type species, such as deep cervical, gastro-orbital, antennal and hepatic grooves, weak postcervical groove, branchiocardiac groove absent, dorsal suture absent, long rostrum with three strong supralateral teeth, weak antennal spine and uropodal exopod with diaeresis. After these remarkable characters in common between *P. pustulosus* and *P. muensteri*, we suppose these forms represent sexual dimorphs of a single species. In fact, in Recent glypheid *Neoglyphea inopinata*, and other fossil glypheids, another group of decapods, the sexual dimorphism also affects the lengths of pereiopod I and its articles, with the longer ones are developed in the female (Forest & de Saint Laurent, 1981, 1989). Thus we suppose *P. pustulosus* is the male and *P. muensteri* the female form (see also the sexual dimorphs in *Cycleryon* Glaessner, 1965, and *Mecochirus* Germar, 1827, in this paper).

Family Stenochiridae Beurlen, 1930

Discussion. Beurlen (1930) established the family Stenochiridae that includes *Stenochirus* Oppel, 1861, without defining its diagnostic characters. The author in fact based this species mainly on the characters of the monotypic *Stenochirus suevicus* Quenstedt, 1867 (Germany – Aalenian), despite *S. angustus* Münster, 1839, the type species of the genus. *Stenochirus suevicus* became later type species of the genus *Palaeophoberus* Glaessner, 1932. By the study of two very well preserved specimens (n. cat. 9706, 9836 – Wulf collection), it was possible to frame for the first time the diagnosis of this family. Thus we do not follow the ascription of *Stenochirus* in Chilenophoberidae by Tshudy & Babcock (1997).

Diagnosis: carapace cylindrical laterally flattened; rostrum long with four supralateral teeth; two dentate carinae in antennal region; cervical groove deep; branchiocardiac groove weak ; pereiopods I-III chelate; pereiopod

I larger and stronger than pereiopods II-III; pereiopods II-V weak with slender and elongate segments; pereiopods II-III weak bearing very small chelae; somite I remarkably smaller than the others; expanded pleura of somite II not overlapping that of somite I; uropodal exopod with diaeresis.

Genus *Stenochirus* Oppel, 1861

Type species: *Bolina angusta* Münster, 1839
Solnhofen species: *Stenochirus angustus* (Münster, 1839); *Stenochirus mayeri* Oppel, 1862

Stenochirus angustus (Münster, 1839)
Fig. 8, Pl. III (fig. 1), Pl. XII (figs. 5, 6)

1839 – *Bolina angusta* Münster; p. 24, Pl. 9 (fig. 14)
1853 – *Bolina angusta* Münster *in* Frischmann; p. 26
1862 – *Stenochirus angustus* (Münster) *in* Oppel; p. 20, Pl. 4 (figs. 3-4)
1904 – *Stenochirus angustus* (Münster) *in* Walther; p. 174
1925 – *Stenochirus angustus* (Münster) *in* Van Straelen; p. 131
1929 – *Stenochirus angustus* (Münster) *in* Glaessner; p. 380
1994 – *Stenochirus angustus* (Münster) *in* Frickhinger; p. 127, Fig. 226
1999 – *Stenochirus angustus* (Münster) *in* Frickhinger; p. 44, Fig. 71
2005b – *Stenochirus angustus* (Münster) *in* Schweigert & Garassino; p. 498

The poor state of preservation of the original specimen by Oppel has led to the examination of new specimens from private collections in order to expand the morphological description of *Stenochirus angustus*. Two specimens (n. cat. 9706, 9836 – Wulf collection), preserved in lateral and dorsal views allowed recognition of many important morphological characters in order to give for the first time a detailed description of this species and the systematic position of the genus into the family Astacidae Latreille, 1802.

Diagnosis: as for the genus.

Holotype by monotypy: BSPG AS VII 322 (Münster, 1839 – Pl. 9, fig. 14), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Flonheim near Solnhofen.

Material: Oppel (1862) reported one specimen, the holotype of Münster, ascribed to this species, and housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where today it is still preserved.

BSPG AS VII 322 – Münster (1839), Pl. 9 (fig. 14)
BSPG AS VII 322 – Oppel (1862), Pl. 4 (figs. 3-4) – length of the specimen: 3 cm

Description. Median-sized astacid with smooth exoskeleton.

Carapace. Carapace cylindrical laterally flattened. Rostrum long with four small supralateral teeth directed forward. Cervical groove median and deep. Branchiocardiac groove weak. Two dentate carinae in antennal region. Posterior margin slightly convex. Ocular incision small, and narrow. Dorsal surface of carapace smooth.

Abdomen. Somite I remarkably smaller than the others. Somites II-VI subrectangular of equal length, rounded pleurae, and with smooth tergal surface. Pleura of somite II subrounded overlapping that of somite III. Telson subrectangular with a weak median longitudinal groove, two pairs of small median longitudinal spines on dorsal surface, and two oblique carinae originating in the proximal part of dorsal surface terminating with a small distal spine on the lateral margin. Protopod subrectangular. Uropodal endopod with a weak longitudinal median carina. Uropodal exopod with a weak longitudinal median carina, one small distal spine on the outer margin, and rounded diaeresis.

Cephalic appendages. Eyestalk short. Antennular articles thin of which the distal one carries two elongate multiarticulate flagella of equal length. Antennal articles strong and stout of which the distal one carries a strong elongate multiarticulate flagellum of the same body length. Scaphocerite triangular with pointed distal extremity.

Thoracic appendages. Pereiopod I with very elongate and slender chela. Movable and fixed fingers of the same length with curved distal extremity. Inner margins of movable and fixed fingers with row of thin and elongate teeth of the same length directed forward. Upper margin of merus with a row of small tubercles. Dorsal surface of propodus with a strong median longitudinal carina. Upper and lower margins of merus and carpus of pereiopod I with a row of strong spines directed forward. Pereiopods II-V weak bearing elongate and slender articles. Pereiopods II-III with remarkably very small chelae. Pereiopods IV-V achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. The systematic position of *Stenochirus* Oppel, 1861, was uncertain for a long time. Beurlen (1928, 1930) established the subfamily Stenochirinae originally and the family Stenochiridae later, justifying it on the basis of morphological characters that were different from the other astacideans. Glaessner (1929, 1969) included *Stenochirus* in the family Erymidae Van Straelen, 1924, originally and later he did not include this genus in any known family of the infraorder Astacidea Latreille, 1803.

The study of the original and new specimens permitted recognition of some morphological characters, such as weak pereiopods II-V bearing slender and elongate articles, pereiopods II-III with remarkably small chelae, somite I remarkably smaller than the others, and subrounded pleura of somite II overlapping that of somite III, that are typical of *Stenochirus* and are not observable in the other genera within the infraorder Astacidea in order to attest the original institution of the family by Beurlen.

Moreover, among the genera belonging to the infraorder Astacidea, the above-mentioned characters are also observable in *Uncina* Quenstedt, 1851 (family Uncinidae Beurlen, 1928) recently reviewed by Schweigert *et al.* (2003), even though this genus differs from *Stenochirus* on the basis of the different shape and morphology of the chela of pereiopod I.

Today, the family Stenochiridae Beurlen, 1930, previously known only in the Upper Jurassic (Tithonian) of Germany, includes three species, *S. angustus* Münster, 1839, *S. mayeri* Oppel, 1862, and *S. vahldieki* Schweigert, Garassino & Riou, 2006, from the Callovian of France (Schweigert *et al.*, 2006).

Stenochirus mayeri Oppel, 1862
Fig. 2, Pl. XIII (figs. 1, 2)

1862 – *Stenochirus Mayeri* Oppel; p. 20, Pl. 4 (figs. 1-2)
1904 – *Stenochirus Meyeri* Oppel *in* Walther; p. 175
1925 – *Stenochirus Meyeri* Oppel *in* Van Straelen; p. 131
1929 – *Stenochirus Meyeri* Oppel *in* Glaessner; p. 380
1969 – *Stenochirus meyeri* Oppel *in* Glaessner; R 460, Text-fig. 267/2
1994 – *Stenochirus meyeri* Oppel *in* Frickhinger; p. 127, Fig. 227

Lectotype: BSPG AS I 673 (Oppel, 1862 – Pl. 4, figs. 1-2), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Remark: The correct original spelling of this taxon is "*mayeri*". An according to the original hand-written label by Oppel this species was dedicated to Charles Mayer-Eymar, not to Hermann v. Meyer.

Material: Oppel (1862) reported one specimen, ascribed to this species, and housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS I 673 – Oppel (1862), Pl. 4 (figs. 1-2) – length of the specimen: 3 cm

Discussion. This species was described by Oppel (1862) on one specimen in ventral view. Even though, the poor state of preservation of the original specimen made difficult to observe the morphological characters of *Stenochirus* Oppel, 1861, pereiopod II with remarkably small chela, pleura of somite II overlapping that of somite III, and uropodal exopod with small spine in the distal part of lateral margin are enough to validate its ascription to this genus. However, it is difficult to develop a morphological description of this species because it is preserved in ventral view. We agree with Oppel in regard to its systematic validity because the shape of the chela of pereiopod I is different from that of *S. angustus* Münster, 1839 (Fig. 2). In fact, Oppel's species exhibits a slender, slightly curved propodus of the chela of pereiopod I with the movable finger longer than fixed finger. Münster's species has a stout and straight propodus of chela of pereiopod I with movable and fixed fingers of the same length. In both species, the inner margins of movable and fixed fingers have a row of thin and elongate teeth of the same length directed forward. Only the discovery of well preserved specimens will make possible a complete morphological description of this species.

Fig. 2 – *Stenochirus mayeri* Oppel, 1862, chela of pereiopod I, line drawing (F. Fogliazza).

Family Glypheidae Winckler, 1883
Genus *Glyphea* v. Meyer, 1835

Type species: *Palinurus regleyanus* Desmarest, 1822
Solnhofen species: *Glyphea pseudoscyllarus* (Schlotheim, 1822); *Glyphea tenuis* Oppel, 1860

Glyphea pseudoscyllarus (Schlotheim, 1822)
Fig. 9, Pl. III (fig. 2), Pl. XIII (fig. 3)

1822 – *Macrourites pseudoscyllarus* Schlotheim; p. 36, Pl. 12 (fig. 5)
1829 – *Scyllarus dubius* Holl; p. 151
1839 – *Orphnea pseduoscyllarus* Münster; p. 39, Pl. 14 (figs. 1-2)
1839 – *Orphnea striata* Münster; p. 40, Pl. 14 (fig. 3)
1839 – *Orphnea laevigata* Münster; p. 41, Pl. 14 (fig. 5)
1839 – *Orphnea pygmaea* Münster; p. 42, Pl. 14 (fig. 6)
1839 – *Brisa dubia* Münster; p. 46, Pl. 15 (figs. 4-5?)
1839 – *Brisa lucida* Münster; p. 46, Pl. 15 (fig. 3)
1853 – *Orphnea pseudoscyllarus* Münster *in* Frischmann; p. 29
1853 – *Orphnea striata* Münster *in* Frischmann; p. 29
1860 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Oppel; p. 110
1862 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Oppel; p. 72, Pl. 18 (fig. 2), Pl. 19 (figs. 1-5)
1883 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Winckler; p. 26, Figs. 4, 6
1904 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Walther; p. 174
1922 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Van Straelen; p. 1224-1226
1925 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Van Straelen; p. 192, Text-fig. 94
1928 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Beurlen; p. 140
1929 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Glaessner; p. 189
1969 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Glaessner; R 463
not 1994 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Frickhinger; p. 120, Fig. 207 = *G. tenuis*
2001 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Dietl & Schweigert; p. 55, Text-fig. 90

Diagnosis: carapace cylindrical laterally flattened; rostrum very short with curved distal extremity; cervical and branchiocardiac grooves deep; postcervical groove weak, joined to branchiocardiac groove near their lower

ends; antennal, hepatic, and ventral grooves weak; three/four carinae tuberculate extend parallel in gastric and antennal regions; pereiopod I subchelate; pereiopods II-V achelate; uropodal exopod with diaeresis.

Holotype: *Macrourites pseudoscyllarus* (= *Glyphea pseudoscyllarus*), MNHB K 43 MB.A. 255 (Schlotheim, 1822 – Pl. 12, fig. 5; length of the specimen: 5 cm), housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Stratigraphic range: Upper Jurassic (upper Kimmerdigian – lower Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported 50 specimens belonging to this species, so divided: 16 from the Redenbacher collection and 34 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied the holotype by Schlotheim, housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, and nine specimens of this original sample, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified one specimen, illustrated by Münster (1839) and Oppel (1862) and seven specimens, illustrated by Oppel (1862). Six specimens without catalogue numbers were identified as belonging to original collections based upon the 19th century labels. We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 730 – Münster (1839), Pl. 14 (fig. 2)
BSPG AS VII 730 – Oppel (1862), Pl. 19 (fig. 2) – incomplete specimen
BSPG AS I 974 – Oppel (1862), Pl. 19 (fig. 3) – length of the specimen: 4 cm
BSPG AS I 976 – Oppel (1862), Pl. 19 (fig. 4) – length of the specimen: 3 cm
BSPG AS VII 1429 – Oppel (1862), Pl. 19 (fig. 1) – length of the specimen: 5 cm
BSPG AS I 975 – Oppel (1862), Pl. 19 (fig. 5) – length of the specimen: 2.5 cm
BSPG AS VII 732 – Oppel (1862), Pl. 14 (fig. 5) – length of the specimen: 2 cm
BSPG AS VII 733 – Oppel (1862), Pl. 14 (fig. 6) – length of the specimen: 1 cm
BSPG AS VII 731 – Oppel (1862), Pl. 14 (fig. 3) – length of the specimen: 4.5 cm

Description. Median-sized glypheid with strongly tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened and strongly tuberculate. Rostrum very short and edentate with curved distal extremity. Cervical and branchiocardiac grooves deep. Postcervical groove weak, joined to branchiocardiac groove near their lower ends. Antennal, hepatic, and ventral grooves weak. Antennal spine well developed. Three/four longitudinal carinae strongly tuberculate extend parallel in gastric and antennal regions. Ocular incision narrow with weakly developed antennal and ptergostomial angles.

Abdomen. Somite I-V subrectangular of equal length and with tuberculate tergal surface. Somites I-V with subtriangular pleurae. Telson subrectangular with rounded distal extremity and three tuberculate carinae extending its total length. Protopod subrectangular. Uropodal endopod smooth. Uropodal exopod with weak median longitudinal groove, marked by two rows of spines, two different distal spines on the outer margin (one longer and one shorter), outer margin with small tubercules, and rounded diaeresis with upper serrate margin.

Cephalic appendages. Eyestalk very elongate and strong. 3rd maxilliped very elongate with first article having a strong distal spine on the outer margin and second article with two strong distal spines on the outer margin respectively. Antennular articles thin and elongate of which the distal one carries two multiarticulate flagella of equal length. 1st and 3rd antennal articles short, 2nd antennal article very elongate with dorsal surface covered with rows of strong parallel spines. Multiarticulate flagellum elongate, twice the body length. Scaphocerite triangular with pointed distal extremity and lower margin with a row of thin and elongate spines.

Thoracic appendages. Pereiopod I subchelate with strong, elongate subrectangular merus and propodus and short subtriangular carpus. Movable finger thin and elongate with tuberculate dorsal surface and serrate upper and lower margins. Lower margin of propodus with strong spines of equal length in proximal and medial parts; distal part with two spines, first stronger and more elongate than second. Dorsal surface of merus, carpus, and propodus covered with strong spines, located along margins in merus, and in parallel rows in carpus and propodus. Pereiopods II-V achelate. Lower margin of merus and carpus of pereiopods II-IV with short spines.

Abdominal appendages. Pleopods with an unsegmented peduncle which carries two elongate multiarticulate flagella.

Discussion. Feldmann & de Saint Laurent (2002) gave a check list of 29 species included in *Glyphea* v. Meyer, 1835. Among these species, *G. squamosa* (Münster, 1839), is now considered the type species of *Squamosoglyphea* Beurlen, 1930 (see the description and discussion in Schweigert & Garassino, 2005, and below). Moreover, the authors did not consider seven species, described by Damborenea & Mancenido (1987), Garassino (1996, 1997, 2000, 2001), Polz (2000), and Schweitzer & Feldmann (2001): *G. eureka* Damborenea & Mancenido, 1987, *G. tricarinata* Garassino, 1996, *G. tonelloi* Garassino, 1997, *G. rigoi* Garassino, 2000, *G. viohli* Polz, 2000, *G. damesi* Garassino, 2001, and *G. michelae* Schweitzer & Feldmann, 2001.

As reported by Glaessner (1929), *Glyphea* may include more species. However, since this genus has never been reviewed, probably many species could be synonym for some morphological characters, such as the path of the grooves, the number of carinae in gastric and antennal regions and the structure of pereiopod I. Unfortunately, this review is made difficult for the problems of finding the original samples and for the loss of many original specimens.

On the basis of this reflection, we consider Feldmann & de Saint Laurent's paper as the most updated paper known to date. So today, *Glyphea* includes 36 species from the Upper Triassic (Norian) to Eocene (Bartonian) of Europe (Germany, France, England, Poland, Italy and Spain), Lebanon, East Africa, North and South America, New Zealand, Australia, and Antarctic Peninsula.

Glyphea tenuis Oppel, 1861
Fig. 9, Pl. IV (fig. 1), Pl. XIII (fig. 4)

1861 – *Glyphea tenuis* Oppel; p. 110
1862 – *Glyphea tenuis* Oppel; p. 76, Pl. 20 (figs. 2-3)
1883 – *Glyphea tenuis* Oppel *in* Winckler; p. 27, Fig. 5
1904 – *Glyphea tenuis* Oppel *in* Walther; p. 174
1994 – *Glyphea pseudoscyllarus* (Schlotheim) *in* Frickhinger; p. 120, Fig. 207
1994 – *Glyphea tenuis* Oppel *in* Frickhinger; p. 120, Fig. 208
2005b – *Glyphea tenuis* Oppel *in* Schweigert & Garassino; p. 498

Diagnosis: carapace cylindrical laterally flattened; rostrum short and edentate with curved distal extremity; cervical and branchiocardiac grooves deep; postcervical groove weak; antennal, hepatic, and ventral grooves weak; one/two longitudinal carinae weak extend parallel in gastric and antennal regions; pereiopod I subchelate; pereiopods II-V achelate; uropodal exopod with diaeresis.

Holotype by monotypy: BSPG AS VIII 95 (Oppel, 1862 – Pl. 20, figs. 2-3) housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Eichstätt.

Material: Oppel (1862) reported one specimen, ascribed to this species, and housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS VIII 95 – Oppel (1862), Pl. 20 (figs. 2-3) – length of the specimen: 4 cm

One specimen (n. cat. 9911 – Wulf collection) was used to describe the tail fan, poorly preserved in the original specimen.

Description. Median-sized glypheid with finely tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened and finely tuberculate. Rostrum short and edentate with curved distal extremity. Cervical and branchiocardiac grooves deep. Postcervical groove weak. Antennal, hepatic, and ventral grooves weak. One/two longitudinal carinae extend parallel in gastric and antennal regions. Ocular incision narrow with weakly developed antennal and ptergostomial angles.

Abdomen. Somites I-V subrectangular of equal length and with smooth tergal surface. Pleurae of somites I-V ending with a point in the median part. Telson subrectangular with rounded distal extremity. Protopod subrectangular. Uropodal endopod with weak longitudinal carina. Uropodal exopod with weak longitudinal carina, strong distal spine in the outer margin, and rounded diaeresis.

Cephalic appendages. Eyestalk elongate and strong. 3rd maxilliped not preserved. Antennular articles thin and elongate of which the distal one carries two multiarticulate flagella of equal length. 1st and 3rd antennal articles short and 2nd antennal article very elongate. Multiarticulate flagellum elongate, twice the body length. Scaphocerite triangular with pointed distal extremity.

Thoracic appendages. Pereiopod I subchelate with short subrectangular merus and propodus and short subtriangular carpus. Movable finger thin and elongate with smooth dorsal surface. Lower margin of propodus with two/three strong spines of equal length distally. Dorsal surface of merus, carpus, and propodus tuberculate. Pereiopods II-V achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. Oppel (1862) pointed out the main morphological differences of this species respect to *G. pseudoscyllarus* (Schlotheim, 1822) in order to justify its institution: smooth exoskeleton, shorter antennal articles and shorter eyestalk. The study of the original specimen confirmed the systematic validity of *G. tenuis* Oppel, 1860: postcervical and branchiocardiac grooves extend parallel without joining near their lower ends, as in *G. pseudoscyllarus*; one/two weak longitudinal carinae in gastric and antennal regions unlike *G. pseudoscyllarus* in which three/four tuberculate carinae are present in these regions; different shape of pereiopod I with shorter merus and propodus and dorsal surface of carpus and propodus without strong spines arranged in parallel rows, as in *G. pseudoscyllarus*; merus and carpus of pereiopods II-IV without spines along the outer margins, well developed instead in *G. pseudoscyllarus*.

Genus *Squamosoglyphea* Beurlen, 1930

Type species: *Glyphea dressieri* v. Meyer, 1840 (for correct spelling of this taxon see Schweigert & Garassino, 2005a)

Squamosoglyphea squamosa (Münster, 1839)
Fig. 9, Pl. IV (fig. 2), Pl. XIII (fig. 5)

1839 – *Orphnea squamosa* Münster; p. 41, Pl. 14 (fig. 4)
1853 – *Orphnea squamosa* Münster *in* Frischmann; p. 29
1854 – *Orphnea squamosa* Münster *in* Pictet; p. 449, Pl. 42 (fig. 9)
1861 – *Glyphea squamosa* (Münster) *in* Oppel; p. 110
1862 – *Glyphea squamosa* (Münster) *in* Oppel; p. 75, Pl. 20 (fig. 1)
1904 – *Glyphea squamosa* (Münster) *in* Walther; p. 174
1925 – *Glyphea squamosa* (Münster) *in* Van Straelen; p. 189
1928 – *Glyphea squamosa* (Münster) *in* Beurlen; p. 136
1929 – *Glyphea squamosa* (Münster) *in* Glaessner; p. 191
1961 – *Glyphea squamosa* (Münster) *in* Martin; p. 70
1973 – *Glyphea squamosa* (Münster) *in* Förster; p. 34
2001 – *Glyphea squamosa* (Münster) *in* Schweitzer & Feldmann; p. 177
2005a – *Squamosoglyphea squamosa* (Münster) *in* Schweigert & Garassino; p. 274, Figs. 1-2

The poor state of preservation of the only original specimen, ascribed to this species, makes it difficult to extend its morphological description over the original one by Münster.

The possibility to clean the tail fan allowed description of it for the first time. Some more details became obvious from a topotype.

Diagnosis: carapace cylindrical laterally flattened having wide superimposed scales; rostrum short and edentate; cervical, postcervical, and branchiocardiac grooves weak; pereiopod I subchelate with propodus longer than wide, spineless on the lower margin; uropodal exopod with diaeresis.

Holotype by monotypy: BSPG AS VII 734 (Münster, 1839 – Pl. 14, fig. 4), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian).

Type locality: Kelheim (after lithology; originally labelled "Solnhofen").

Material: Oppel (1862) reported two specimens belonging to this species, so divided: one from the Redenbacher collection and one (the original of Münster) from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied the holotype by Münster, illustrated by Münster (1839) and Oppel (1862), and the other specimen from the Redenbacher collection in the Museum für Naturkunde der Humboldt-Universität in Berlin.

BSPG AS VII 734 – Münster (1839), Pl. 14 (fig. 4)

BSPG AS VII 734 – Oppel (1862), Pl. 20 (fig. 1) – length of the specimen: 5 cm

MNHB MB.A.1106 – Oppel (1862), p. 75, not figured – length of the specimen: 4.2 cm

Description. Small-sized glypheid with exoskeleton characterized by imbricated scales. The holotype is dorsally embedded, whereas the second specimen is embedded in oblique view.

Carapace. Carapace cylindrical laterally flattened having wide superimposed scales in cardiac and branchial regions reducing in size toward gastric and antennal regions. Rostrum short and edentate. Cervical, postcervical, and branchiocardiac grooves weak. Ocular incision narrow with weakly developed antennal and ptergostomial angles. Posterior margin sinuous with a thin marginal carina.

Abdomen. Somites I-V subrectangular of equal length and with smooth tergal surface. Pleurae of somites I-V ending with a point in the median part. Somite VI subrectangular longer than the previous ones. Telson subrectangular with rounded distal extremity. Dorsal surface of telson with a pair of narrow and raised carinae originating in proximal part of lateral margins and converging in the middle without joining. Rounded basal tubercle in the middle between the two carinae. A pair of grooves narrow and weak arise from the distal end of the carinae diverging toward the distal extremity. Protopod subrectangular. Uropodal endopod with weak longitudinal groove marked with two rows of rounded tubercles. Uropodal exopod with deep longitudinal groove marked with two rows of rounded tubercles, strong spine in the distal part of outer margin, and subrounded diaeresis. In the ventral part of the tergum of the somites, forming forwardly directed lobes are developed, located just above the pleurae, like in the reconstruction of *S. udressieri* by Oppel (1862 – Pl. 16, fig. 7).

Cephalic appendages. Merocerite of antennae strongly elongate with four thin and elongate spines along lower margin. Carpocerite of antennae short with elongate multiarticulate flagellum (total length unknown). Antennulae poorly preserved, both flagella of different length (ca. 5 mm vs. 6 mm).

Thoracic appendages. Pereiopod I subchelate with propodus longer than wide and spineless lower margin. Movable finger thin and elongate with a median groove. Carpus short and subtriangular with spineless lower margin. Surface of propodus with irregularly arranged scale-like rounded tubercles with forwardly directing tips. Surface of carpus with scale-like tubercles exhibiting multiple forwardly directing tips, especially in the distal part. Pereiopods II-V achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. Beurlen (1930) based a new subgenus on the closely related *S. dressieri* (v. Meyer, 1840) – for the correct spelling of the latter see Schweigert & Garassino (2005a). The presence of superimposed scales instead of tubercles is so different from *Glyphea sensu stricto* that we give genus rank to this taxon. Besides *S. squamosa*, two other species of this genus occur in the Upper Jurassic lithographic limestones of S Germany which were described separately (Schweigert & Garassino, 2005).

Family Mecochiridae Van Straelen, 1924
Genus *Mecochirus* Germar, 1827

Type species: *Macrourites longimanatus* Schlotheim, 1820

Solnhofen species: *Mecochirus longimanatus* (Schlotheim, 1820); *Mecochirus dubius* (Münster, 1839)

Mecochirus longimanatus (Schlotheim, 1820) (♀)
Fig. 9, Pl. V (fig. 1), Pl. XIII (fig. 6), Pl. XIV (fig. 1)

1820 – *Macrourites longimanatus* Schlotheim; p. 38

1822 – *Macrourites longimanatus* Schlotheim; p. 33

1822 – *Macrourites longimanatus* Schlotheim *in* Brogniart & Desmarest; p. 136, Pl. 5 (fig. 10)

1823 – *Macrourites longimanatus* Schlotheim; p. 56

1825 – *Palaemon longimanatus* Krüger; p. 130

1827 – *Mecochirus locusta* Germar; p. 102

1827 – *Mecochirus Bajeri* Germar; p. 103, Text-fig. 5, **nov. syn.**

1829 – *Palaemon longimanatus* Krüger *in* Holl; p. 152

1837 – *Megachirus locusta* Bronn; p. 476, Pl. 27 (fig. 1)

1837 – *Megachirus longimanus* Bronn; p. 476, Text-fig. 16a

1839 – *Megachirus brevimanus* Münster; p. 34, Pl. 13 (figs. 1?, 2, 3), **nov. syn.** (♂)

1839 – *Megachirus locusta* Bronn *in* Münster; p. 31, Pl. 11 (figs. 1-5)

1839 – *Megachirus Bajeri* (Germar) *in* Münster; p. 33, Pl. 12 (figs. 1-5), Pl. 13 (figs. 6-7)

1839 – *Megachirus fimbriatus* Münster; p. 35

1839 – *Megachirus intermedius* Münster; p. 35, Pl. 13 (figs. 4?, 5)

1839 – *Pterochirus remimanus* Bronn *in* Münster; p. 27, Pl. 16 (figs. 1-2)

1839 – *Pterochirus elongatus* Münster; p. 28, Pl. 16 (fig. 3)

1839 – *Orphnea longimanus* Münster; p. 42, Pl. 14 (fig. 7)

1848 – *Megachirus locusta* Bronn; p. 708

1850 – *Mecochirus locusta* Germar *in* Quenstedt; p. 196, Pl. 2 (figs. 1-3)

1853 – *Mecochirus locusta* Germar *in* Bronn; p. 418, Pl. 27 (fig. 1, 16a)

1862 – *Mecochirus longimanus* (Schlotheim) *in* Oppel; p. 82, Pl. 22 (fig. 4), Pl. 23 (fig. 1)

1862 – *Mecochirus Bajeri* Germar *in* Oppel; p. 83, Pl. 23 (fig. 2)

1862 – *Mecochirus brevimanus* (Münster) *in* Oppel; p. 84, Pl. 22 (figs. 5-6)

1904 – *Mecochirus longimanus* (Schlotheim) *in* Walther; p. 174

1904 – *Mecochirus Bajeri* Germar *in* Walther; p. 174
1904 – *Mecochirus brevimanus* (Münster) *in* Walther; p. 174
1925 – *Mecochirus longimanatus* (Schlotheim) *in* Van Straelen; p. 218
1929 – *Mecochirus longimanatus* (Schlotheim) *in* Glaessner; p. 250
1929 – *Mecochirus Bajeri* Germar *in* Glaessner; p. 249
1929 – *Mecochirus brevimanus* (Münster) *in* Glaessner; p. 249
1969 – *Mecochirus longimanatus* (Schlotheim) *in* Glaessner; R 464, Text-fig. 270/1
1971 – *Mecochirus longimanatus* (Schlotheim) *in* Förster; p. 403, Text-fig. 5
1994 – *Mecochirus longimanatus* (Schlotheim) *in* Frickhinger; p. 122, Figs. 214-216
1994 – *Mecochirus bajeri* Germar *in* Frickhinger; p. 122, Fig. 212
1994 – *Mecochirus brevimanus* (Münster) *in* Frickhinger; p. 122, Fig. 213
1996 – *Mecochirus* sp. *in* Röper, Rothgaenger & Rothgaenger; p. 72, Fig. 89
1999 – *Mecochirus brevimanus* (Münster) *in* Frickhinger; p. 43, Fig. 68
2000 – *Mecochirus brevimanus* (Münster) *in* Röper, Rothgaenger & Rothgaenger; p. 91, Fig. 105
2005b – *Mecochirus longimanatus* (Schlotheim) *in* Schweigert & Garassino; p. 498

Diagnosis: carapace cylindrical laterally flattened; rostrum short and edentate; cervical groove deep in the third anterior of carapace; antennal and hepatic grooves deep; postcervical and branchiocardiac grooves weak extending parallel; three carinae strong and tuberculate in the gastric and antennal regions; extraordinary extension of pereiopod I subchelate; pereiopod II subchelate; pereiopods III-V achelate; uropodal exopod with diaeresis.

Neotype (original type series of Schlotheim lost): *Macrourites longimanatus* (= *Mecochirus longimanatus*), BSPG AS V 45, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Our studies revealed that *Mecochirus bajeri* from Solnhofen and figured by Germar (1827 – Pl. 1, fig. 5) is synonym with *Mecochirus longimanatus*, as discussed below. The monotypic holotype was not traceable in the collection of the Institut für Geowissenschaften in Halle/Saale (Germany) (Dr. N. Hauschke, Halle, pers. com.), and it is probably lost.

Our studies revealed that *Megachirus brevimanus* from Eichstätt and figured by Münster (1839 – Pl. 13, fig. 2) is synonym with *Mecochirus longimanatus*, as discussed below. This specimen, BSPG ASVII 739, is the lectotype of Münster's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – lower Tithonian).

Type locality: Solnhofen.

Material: Schlotheim (1820) introduced the name reported on a sample of three specimens and commented that this species is the most common one in the Solnhofen shales. A neotype was selected because none of the specimens of Schlotheim collection was traceable in the Museum für Naturkunde in Humboldt University in Berlin. Oppel (1862) reported 103 specimens belonging to this species, so divided: 30 from the Redenbacher collection and 73 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample six specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified three specimens, illustrated by Münster (1839) and three specimens, illustrated by Oppel (1862). Two specimens were identified as belonging to Münster's original collection thanks to the 19th century labels. We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 745 – Münster (1839), Pl. 11 (fig. 3) – length of the specimen: 6 cm
BSPG AS VII 746 – Münster (1839), Pl. 11 (fig. 1) – length of the specimen: 9 cm
BSPG AS VII 748 – Münster (1839), Pl. 16 (fig. 3) – length of the specimen: 4 cm
BSPG AS V 45 – Oppel (1862), Pl. 22 (fig. 4) – length of the specimen: 10 cm
BSPG AS I 780 – Oppel (1862), Pl. 22 (fig. 5) – length of the specimen: 5 cm
BSPG AS VI 31 – Oppel (1862), Pl. 23 (fig. 1) – length of the specimen: 8 cm

Oppel (1862) reported 70 specimens which he assigned to *Mecochirus bajeri* Germar, 1827, so divided: 20 from the Redenbacher collection and 50 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample nine specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified eight specimens, illustrated by Münster (1839), and one specimen, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 735 – Münster (1839), Pl. 16 (fig. 2) – length of the specimen: 5 cm
BSPG AS VII 736 – Münster (1839), Pl. 16 (fig. 1) – incomplete specimen
BSPG AS VII 738 – Münster (1839), Pl. 12 (fig. 5) – length of the specimen: 7 cm
BSPG AS VII 741 – Münster (1839), Pl. 12 (fig. 3) – length of the specimen: 6 cm
BSPG AS VII 742 – Münster (1839), Pl. 12 (fig. 4) – incomplete specimen
BSPG AS VII 743 – Münster (1839), Pl. 13 (fig. 4) – length of the specimen: 6 cm
BSPG AS VII 744 – Münster (1839), Pl. 13 (fig. 5) – length of the specimen: 6 cm
BSPG AS VII 749 – Münster (1839), Pl. 13 (fig. 6) – length of the specimen: 6 cm
BSPG AS I 981 – Oppel (1862), Pl. 23 (fig. 2) – length of the specimen: 8 cm

Oppel (1862) reported 50 specimens which he assigned to *Mecochirus brevimanus* (Münster, 1839) without pointing out how many specimens belonged to the Redenbacher collection and to the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied three specimens of this original sample, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich and illustrated by Münster (1839). One specimen was identified as belonging to Münster's original collection thanks to the 19th century labels. We report the list of the specimens, studied by Münster:

BSPG AS VII 739 – Münster (1839), Pl. 13 (fig. 2) – length of the specimen: 7 cm
BSPG AS VII 740 – Münster (1839), Pl. 13 (fig. 1) – length of the specimen: 10 cm

BSPG AS VII 750 – Münster (1839), Pl. 13 (fig. 3) – length of the specimen: 4 cm

Description. Large mecochirid with slightly tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened having straight dorsal margin. Rostrum short and edentate. Cervical groove deep in the third anterior of carapace. Antennal and hepatic grooves deep. Postcervical and branchiocardiac grooves weak and parallel. Three carinae strong and tuberculate in gastric and antennal regions. Ocular incision narrow, and shallow.

Abdomen. Somites I-VI subrectangular of equal length with slightly tuberculate tergal surface. Pleurae of somites I-V subtriangular with serrate margins. Telson subrectangular with one raised tubercle in proximal part of dorsal surface, a pair of thin spine in the distal part of lateral margins, a thin median spine on lower margin and rounded distal extremity. Protopod subrectangular. Uropodal endopod with a strong median longitudinal carina. Uropodal exopod with a strong median longitudinal carina and a rounded diaeresis with upper serrate margin having one longer median spine. Fringed lower margins of uropodal endopod and exopod.

Cephalic appendages. Eyestalk short. Antennulae not preserved. Antennal articles strong, and elongate of which the distal one carries a strong elongate multiarticulate flagellum, twice the body length. Scaphocerite triangular with pointed distal extremity.

Thoracic appendages. Extraordinary extension of pereiopod I subchelate. Possibly this is a character of female specimens (see *M. brevimanus* below supposed to be the corresponding male). Lower margin of propodus with one strong and sharp distal tooth. Movable finger strong and elongate with tuberculate upper and lower margins. Dorsal surface of movable finger with two parallel rows of small tubercles. Fringed lower margin of merus, carpus, and propodus of pereiopod I. Fringed upper and lower margins of movable finger of pereiopod I. Pereiopod II subchelate with strong and stout propodus. Fringed lower margins of merus, carpus, and propodus of pereiopod II. Pereiopods III-V of equal length and achelate.

Abdominal appendages. Pleopods with an unsegmented peduncle which carries two elongate multiarticulate flagella.

Discussion. Förster (1971) reviewed this genus, including 18 species. Later, Simpson & Middleton (1985), studying a sample of mecochirids from the Lower Cretaceous of England, described the new genus *Meyerella* having as type species *Mecochirus magnus* McCoy, 1849. Moreover, the authors, using as reference Förster (1971), pointed out that *Mecochirus schwarzi* (Kitchin, 1913) is synonym with *Mecochirus rapax* (Harbort, 1905), better referred to *Meyerella*, and *Mecochirus mexicanus* (Rathbun, 1935) and *Mecochirus bolivari* (Van Straelen, 1927) are synonyms of *Meyerella magna* (McCoy, 1849). Finally, the authors pointed out that *Mecochirus ornatus* (Phillips, 1829) was the type species of *Meyeria* McCoy, 1849, and *Mecochirus gracilis* (Glaessner, 1932) belongs to this genus. Today, *Mecochirus* Germar, 1827, known from the Lower Jurassic (Sinemurian) to the Upper Cretaceous (Maastrichtian) of Europe (Germany, France, England and Italy), Greenland, South America (Chile), Antarctic Peninsula and New Zealand, includes fifteen species. Three species are known from the Lower Jurassic: *M. olifex* Quenstedt, 1856 (Germany – Sinemurian), *M. germari* Garassino, 1996 (Italy – Sinemurian), and *M. eckerti* Frentzen, 1937 (Germany – Toarcian). Three species have been recognized from the Middle Jurassic: *M. clypeatus* (Carter, 1898) (England – Bathonian), *M. socialis* (v. Meyer, 1841) (Germany, France, England – Callovian), and *M. pearcei* McCoy, 1849 (England – Oxfordian). Seven species are described from the Upper Jurassic: *M. peytoni* Woodward, 1876 (France, England – Kimmeridgian), *M. leionotus* (Krause, 1891) (Germany – Kimmeridgian), *M. minimus* (Hée, 1924) (France – Kimmeridgian), *M. marwicki* Glaessner, 1960 (New Zealand – Kimmeridgian), *M. chilensis* Förster & Hillebrandt, 1984 (Chile – Kimmeridgian), and *M. longimanatus* (Schlotheim, 1822) (Germany – Tithonian). One is known from the Lower Cretaceous: *M. houdardi* Van Straelen, 1936 (France – Albian), and two are reported from the Upper Cretaceous: *M. crofti* Ball, 1960 (Antarctic Peninsula – Campanian), and *M. rostratus* Collins & Rasmussen, 1992 (Greenland – Maastrichtian).

Germar (1827), describing *Mecochirus bajeri* on one incomplete specimen, pointed out the main morphological differences respect *M. longimanatus*, such as a shorter pereiopod I and the abdomen longer than carapace. Oppel (1862) pointed out that the shorter pereiopod I is the main morphological characters distinguished *M. bajeri* from the type species. However, the study of specimens of *M. longimanatus* and *M. bajeri*, having the same dimensional class, showed that the length of pereiopod I was the same, as well as the length of the abdomen. Moreover, the specimens belonging to *M. bajeri* showed the same morphological characters of the type species, such as the tuberculate longitudinal carinae of carapace, a strong distal spine of the propodus of pereiopod I and the same structure of tail fan, enough to consider it as synonym of *M. longimanatus*, probably a juvenile stage of the type species.

Münster (1839), describing *Megachirus brevimanus*, pointed out the main morphological differences respect *M. longimanatus*, such as the shorter pereiopod I and propodus of pereiopod I shorter than carapace. Apart from these very significant characters, the specimens belonging to *M. brevimanus* exhibit the same morhological characters of the type species, such as the tuberculate longitudinal carinae of carapace, the strong distal spine of the propodus of pereiopod I, and the same structure of tail fan. After these remarkable characters in common between *M. longimanatus* and *M. brevimanus*, we suppose these forms represent sexual dimorphs of a single species. In fact, in Recent glypheid *Neoglyphea inopinata*, the closest living relative of this group of decapods, the sexual dimorphism also affects the lengths of pereiopod I and its articles, with the longer ones are developed in the female (Forest & de Saint Laurent, 1981, 1989). Thus we suppose *M. brevimanus* is the male and *M. longimanatus* the female form.

Mecochirus dubius (Münster, 1839)
Pl. XIV (fig. 2)

1839 – *Pterochirus dubius* Münster; p. 29, Pl. 16 (figs. 4-6)
1840 – *Norna lithophila* Münster; p. 22, Pl. 3 (fig. 9)
1862 – *Mecochirus dubius* (Münster) *in* Oppel; p. 84, Pl. 23 (fig. 3)
1929 – *Mecochirus dubius* (Münster) *in* Glaessner; p. 249-250

Lectotype: BSPG AS I 979 (Oppel, 1862 – Pl. 23, fig. 3), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported 11 specimens belonging to this species from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample three specimens in which we identified two specimens, illustrated by Münster (1839) and one specimen, illustrated by Oppel (1862). Four specimens were identified as belonging to Münster's original collection thanks to the 19th century labels. We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 737 – Münster (1839), Pl. 16 (fig. 6) – length of the specimen: 2 cm

BSPG AS VII 747 – Münster (1839), Pl. 16 (fig. 4) – length of the specimen: 2 cm

BSPG AS I 979 – Oppel (1862), Pl. 23 (fig. 3) – incomplete specimen

Discussion. Münster (1839) justified the institution of this species because pereiopod I is shorter and higher than that of the other species, pointing out the difficulty of giving its morphological description for the fragmentary of the sample. The study of the original specimens still available has pointed out that their poor state of preservation and their ventral view made difficult to give not only a morphological description of *M. dubius*, but also a comparison with the other species belonging to *Mecochirus*. Even though the small sizes of the specimens lead us to think that they could be ontogenetic stages of *M. longimanatus*, it is difficult to assert it.

Infraorder Thalassinidea Latreille, 1831
Superfamily Axioidea Huxley, 1879
Family Axiidae Huxley, 1879
Genus *Etallonia* Oppel, 1861

Type species: *Magila longimana* Münster, 1839

Etallonia longimana (Münster, 1839)
Figs. 3, 9, Pl. XIV (fig. 3)

1839 – *Magila longimana* Münster; p. 25, Pl. 10 (fig. 3)
1861 – *Etallonia longimana* (Münster) *in* Oppel; p. 361
1862 – *Etallonia longimana* (Münster) *in* Oppel; p. 49, Pl. 12 (figs. 5-7)
1904 – *Etallonia longimana* (Münster) *in* Walther; p. 175
1925 – *Etallonia longimana* (Münster) *in* Van Straelen; p. 231, Text-fig. 109
1929 – *Etallonia longimana* (Münster) *in* Glaessner; p. 168
1930 – *Etallonia longimana* (Münster) *in* Beurlen & Glaessner; p. 78
1969 – *Etallonia longimana* (Münster) *in* Glaessner; R 477, Text-fig. 282/4
1994 – *Etallonia longimana* (Münster) *in* Frickhinger; p. 120, Fig. 205
1999 – *Etallonia longimana* (Münster) *in* Polz; p. 34, Text-fig. 2, Pl. 1 (figs. 5-7)
2005b – *Etallonia longimana* (Münster) *in* Schweigert & Garassino; p. 499

The poor state of preservation of the original specimens and the lack of better preserved new specimens did not permit adding new morphological characters to the original description by Münster. In fact, the carapace, cephalic appendages, and tail fan are too poorly preserved to give their description (Fig. 3).

Dignosis: carapace cylindrical laterally flattened; pereiopod I subchelate; pereiopods II with small chela; pereiopods III-V achelate; uropodal exopod with diaeresis.

Lectotype: BSPG AS VII 259 (Münster, 1839 – Pl. 10, fig. 3), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported five specimens belonging to this species, so divided: two from the Redenbacher collection and three from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample two specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified one specimen, illustrated by Münster (1839) and one specimen, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 259 – Münster (1839), Pl. 10 (fig. 3)

BSPG AS VII 259 – Oppel (1862), Pl. 12 (fig. 5) – length of the specimen: 3 cm

BSPG AS VIII 96 – Oppel (1862), Pl. 12 (fig. 7) – length of the specimen: 2 cm

Description. Small-sized axiid with smooth exoskeleton.

Carapace. Carapace cylindrical laterally flattened. Poorly preserved in both specimens.

Abdomen. Somites I-V subrectangular of equal length with rounded pleurae. Somite VI subrectangular longer than the previuos ones. Telson subrectangular with rounded distal extremity. Uropodal exopod with weak longitudinal median carina and rounded diaeresis.

Cephalic appendages. Antennal flagellum elongate.

Thoracic appendages. Pereiopod I stronger than the others and subchelate. Movable finger pointed and curved downward. Lateral spine (= fixed finger) straight and shorter than movable finger. Basal spine in more or less median position, forming with sinus fixed finger. Propodus of pereiopod I with strong longitudinal median carina. Pereiopods II elongate with small chela. Pereiopods III-V elongate and achelate.

Abdominal appendages. Not preserved.

Discussion. *Etallonia*, very rare in the lithographic limestone, was reviewed by Förster (1977). This genus, known only in the Upper Jurassic (Oxfordian – Tithonian) of Germany, Poland, and Great Britain, includes – after Förster (1977) – four species, *E. subtilis* (Krause, 1908) (Poland – Oxfordian), *E. isochela* (Woodward, 1876) (Great Britain – Kimmeridgian), *E. longimana* and *E. hoellorum* Polz, 1999 (Germany – Kimmeridgian/Tithonian).

Förster (1977) synonymized *Etallonia* and *Protaxius*. Maybe he was in error when he made that. The shape of the chelae of *Callianassa isochela* Woodward, 1876 (type species of *Protaxius* Beurlen, 1930) is close to that of *P. suevicus* Beurlen, 1930. Förster (1965) took *P. suevicus* as synonym of *E. suprajurensis* (Quenstedt, 1852). We point out that probably this is not correct because *P. suevicus* lacks the spine on the subchela, typical of *Etallonia*. So Förster's results have to be reviewed. Two indeterminate
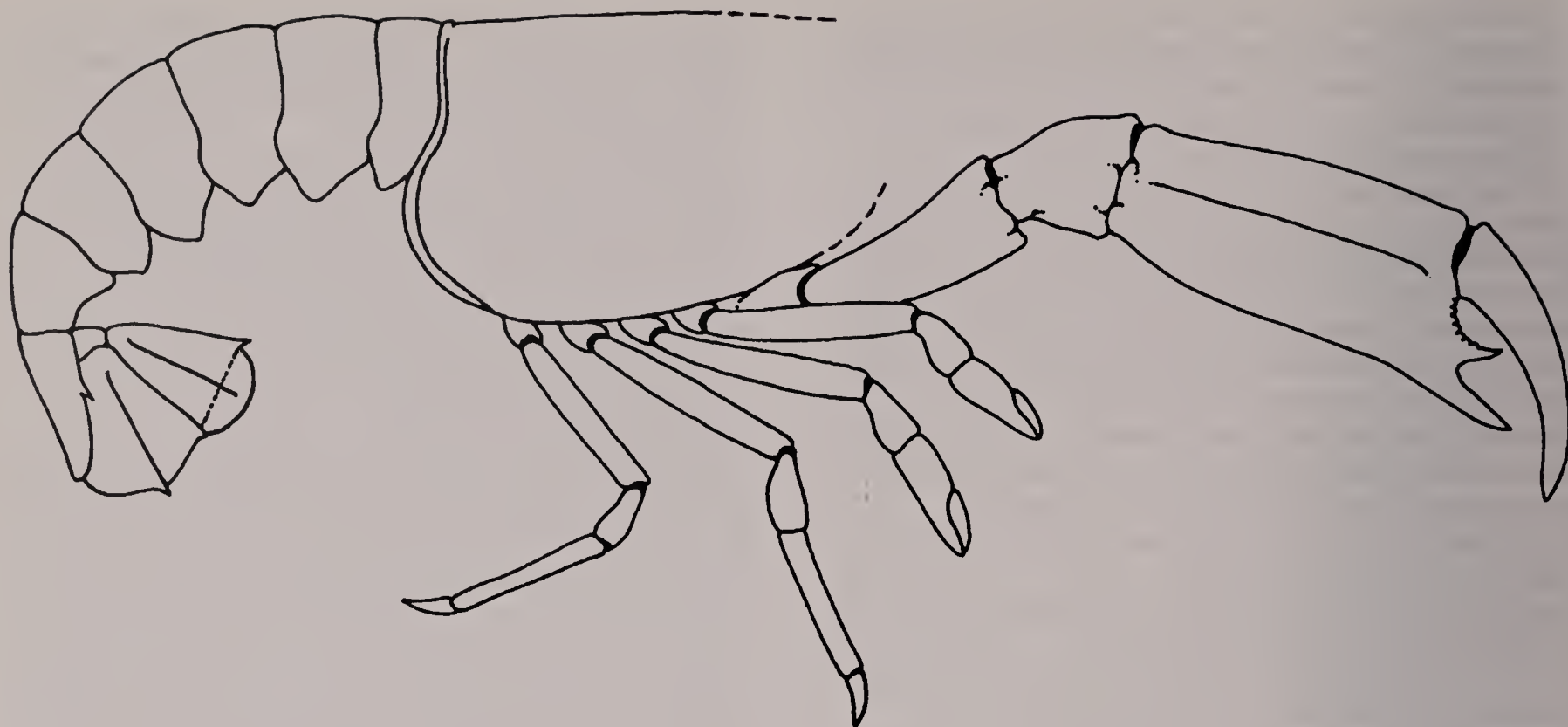
Fig. 3 – *Etallonia longimana* (Münster, 1839), line drawing (F. Fogliazza).

species are known from the Kimmeridgian and Tithonian of Great Britain and Tanzania (Arkell, 1933; Beurlen, 1933). An incompletely known species from the Toarcian of Italy tentatively included in *Etallonia* by Garassino & Teruzzi (2001) probably represents a *Megachela* Schweigert, 2003.

Genus *Magila* Münster, 1839

Type species: *Magila latimana* Münster, 1839

Solnhofen species: *Magila latimana* Münster, 1839; *Magila desmarestii* (Münster, 1839); ?*Magila denticulata* Münster, 1839

Magila latimana Münster, 1839

Figs. 4, 9, Pl. V (fig. 2), Pl. XIV (figs. 4, 5)

1839 – *Magila latimana* Münster; p. 25, Pl. 10 (fig. 2)

1852 – *Pagurus suprajurensis* Quenstedt; p. 265, Pl. 20 (fig. 9) (not fig. 8)

1858 – *Pagurus suprajurensis* Quenstedt; p. 804, Pl. 99 (fig. 20)

1861 – *Magila latimana* Münster *in* Oppel; p. 361

1862 – *Magila latimana* Münster *in* Oppel; p. 48, Pl. 12 (figs. 1-2)

1862 – *Magila suprajurensis* (Quenstedt) *in* Oppel; p. 47

1885 – *Pagurus suprajurensis* Quenstedt; p. 405, Pl. 31 (figs. 37-39) (not fig. 36)

1891 – *Callianassa suprajurensis* (Quenstedt) in Krause; p. 209, Pl. 14 (fig. 4)

1925 – *Magila latimana* Münster *in* Van Straelen; p. 297

1928 – *Magila latimana* Münster *in* Beurlen; p. 185

1928 – *Magila suprajurensis* (Quenstedt) var. *lata* Beurlen; p. 185

1929 – *Callianassa suprajurensis* (Quenstedt) var. *lata* Beurlen *in* Glaessner; p. 92

1930 – *Magila suprajurensis* (Quenstedt) *in* Beurlen; p. 229, Text-fig. 5

1965 – *Magila latimana* Münster *in* Förster; p. 146, Text-fig. 2, Pl. 2 (fig. 7)

1969 – *Magila latimana* Münster *in* Glaessner; R 477, Text-fig. 282/3

1994 – *Magila latimana* Münster *in* Frickhinger; p. 121, Fig. 211

2005b – *Magila latimana* Münster *in* Schweigert & Garassino; p. 499

Diagnosis: Carapace cylindrical laterally flattened; deep cervical groove strongly directed forward; one or two carinae weak in antennal region; rostrum short and edentate; antennal spine well developed; pereiopods I-III chelate; pereiopod I larger and stronger than pereiopods II-III; pereiopods IV-V achelate; uropodal exopod with diaeresis.

Lectotype: BSPG AS VI 26 (Oppel, 1862 – Pl. 12, fig. 2), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: originally labelled as coming from "Solnhofen". According to lithology of the rock matrix containing the lectotype it came from the vicinity of Eichstätt.

Material: Oppel (1862) reported ten specimens belonging to this species, so divided: six from the Redenbacher collection and four from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample four specimens, housed in Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified two specimens, illustrated by Münster (1839) and two specimens, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 199 – Münster (1839), Pl. 10 (fig. 5) – length of the specimen: 2.5 cm

BSPG AS VII 320 – Münster (1839), Pl. 10 (fig. 2) – length of the specimen: 2.5 cm

BSPG AS VI 26 – Oppel (1862), Pl. 12 (fig. 2) – length of the specimen: 2.5 cm

BSPG AS I 674 – Oppel (1862), Pl. 12 (fig. 1b) – incomplete specimen

One specimen (n. cat. 0117 – Wulf collection) was used to describe the carapace and the tail fan, poorly preserved in the original specimens.

Description. Small-sized axiid with weakly tuberculate exoskeleton.

Carapace. Carapace cylindrical laterally flattened. Rostrum short, pointed, and edentate. One or two carinae weak and straight in antennal region. Cervical groove deep and median strongly directed forwards, reducing gastric and antennal regions. Cardiac and branchial regions wide. Antennal spine well developed. Posterior margin strengthened by a thin marginal carina.

Abdomen. Somites I-V subrectangular of equal length with rounded pleurae. Somite VI longer than the previous ones. Telson subtriangular, as long as uropods, with pointed distal extremity. Uropodal endopod with a weak median longitudinal carina ending with a strong spine on lower margin and a strong distal spine on outer margin. Uropodal exopod with a weak median longitudinal carina ending with a small spine on lower margin and a strong distal spine on outer margin. These spines marked a very small diaeresis present only on outer half of lower margin. Outer margin serrate of uropodal exopod (Fig. 4).
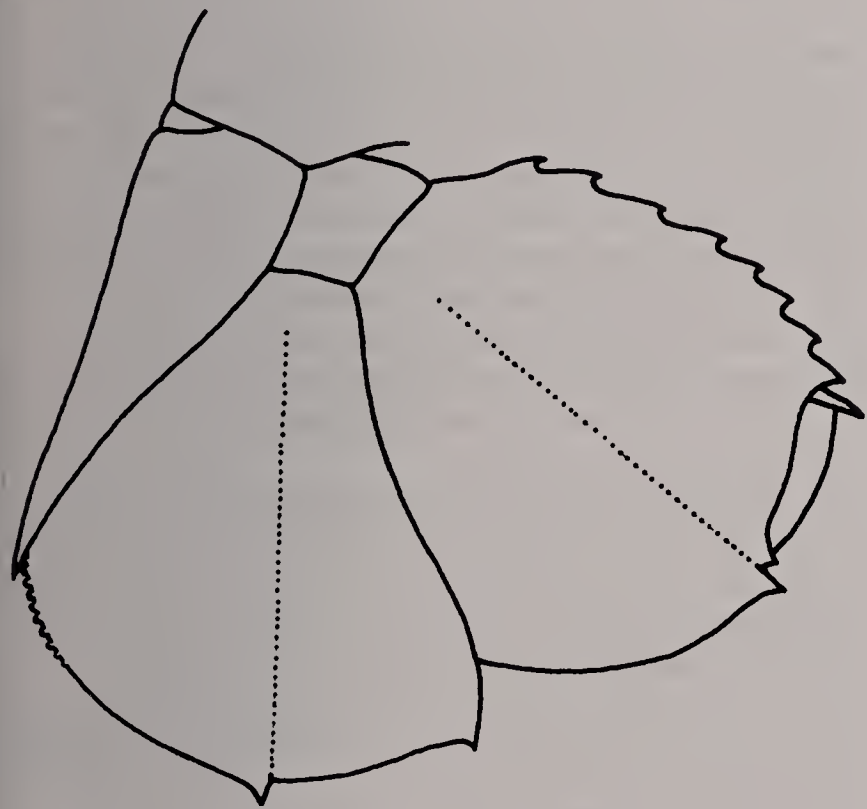
Fig. 4 – *Magila latimana* Münster, 1839, tail fan, line drawing (F. Fogliazza).

Cephalic appendages. Poorly preserved. Antennula with two elongate and thin flagella. Antenna with a very elongate and thick flagellum twice length of body.

Thoracic appendages. 3rd maxilliped not preserved. Pereiopod I with stocky and short chelae with movable and fixed fingers of equal length and with curved distal extremity. Inner margins of movable and fixed fingers. Pereiopods II-III with small and thin chelae. Pereiopods IV-V elongate and achelate. Lower margin of propodus of pereiopods IV-V with a row of thin spines the last ones stronger than the previous ones.

Abdominal appendages. Pleopods with an unsegmented peduncle which carries two elongate multiarticulate flagella.

Discussion. *Magila*, very rare in the lithographic limestone, was reviewed by Förster (1977). This genus, known from the Toarcian to Tithonian (Lower – Upper Jurassic) of Germany, France and Great Britain, includes six species: *M. bonjouri* (Etallon, 1861) (France – Toarcian), *M. pichleri* Oppel, 1862 (Germany, Great Britain – Callovian), *M. straeleni* (Patrulius, 1959) (Romania, Israel – Tithonian), *M. latimana* Münster, 1839, *M. desmarestii* (Münster, 1839), and ?*M. denticulata* Münster, 1839 (Germany – Tithonian). Moreover, Förster (1977) pointed out that *M. prisca* (Krause, 1891) must be considered a synonym of *Callianassa krausei* Böhm, 1911. Finally, *Magila* includes two subspecies, *M. dura bicristata* Förster, 1977 (Poland – Oxfordian) and *M. dura dura* (Moericke, 1889) (Russia – Tithonian).

Magila desmarestii (Münster, 1839)
Pl. XIV (fig. 6), Pl. XV (fig. 1)

1839 – *Aura desmaresti* Münster; p. 26, Pl. 10 (fig. 5)
1854 – *Aura desmarestii* Münster *in* Pictet; p. 454, Pl. 42 (fig. 21)
1862 – *Magila robusta* Oppel; p. 48, Pl. 12 (fig. 3), **nov. syn.**
1925 – *Magila robusta* Oppel *in* Van Straelen; p. 296
1929 – *Magila robusta* Oppel *in* Glaessner; p. 246
2000 – *Magila* cfr. *atimana* Münster *in* Röper, Rothgaenger & Rothgaenger; p. 91, Fig. 106

Holotype by monotypy: BSPG AS VII 199 (Münster, 1839 – Pl. 10, fig. 5), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Our studies revealed that *Magila robusta* from Eichstätt and figured by Oppel (1862 – Pl. 12, fig. 3) is synonym with *Magila desmarestii*, as discussed below. This specimen, AS I 675, is the holotype of Oppel's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported one specimen, ascribed to this species, and housed in Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS VII 199 – Münster (1839), Pl. 10 (fig. 5) – length of the specimen: 3.5 cm

Oppel (1862) reported the presence of only one specimen which he assigned to *Magila robusta* Oppel, 1862, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS I 675 – Oppel (1862), Pl. 12 (fig. 3) – incomplete specimen

Discussion. Münster (1839) described this species on one incomplete, small specimen. Even though, it is ascribed to *Magila* for the typical shape of the chela of pereiopod I, its poor state of preservation did not allow a morphological description of *M. desmarestii* and the lack of diagnostic characters, typical of this species, hardly allow comparison with the other species of the genus.

Oppel (1862) described *Magila robusta* based on one incomplete, small specimen. Even though, it is ascribed to *Magila* for the typical shape of the chela of pereiopod I, its poor state of preservation did not allow writing a

complete morphological description of *M. robusta*. However, the shape of the chelae of pereiopod I fits well with those of *M. desmarestii* in order to suppose both species as synonym.

?*Magila denticulata* Münster, 1839

1839 – *Magila denticulata* Münster; p. 26, Pl. 10 (fig. 4)
1862 – *Magila denticulata* Münster *in* Oppel; p. 46
1925 – *Magila denticulata* Münster *in* Van Straelen; p. 298
1929 – *Eryma* sp. *in* Glaessner; p. 160

Discussion. Münster (1839) described this species based on one incomplete, small specimen from Eichstätt. The loss of this specimen, probably housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, made difficult to give a new morphological description of *Magila denticulata* Münster, 1839, in order to establish its systematic validity, and to compare it with the other species of the genus. So we consider *Magila denticulata* a *nomen dubium*, not being able to establish its validity or its probable synonymy.

As Van Straelen (1925) and Glaessner (1929) pointed out, this species should be ascribed to *Eryma* Meyer, 1840, for the shape of chelae that resembles those of this genus. The drawing by Münster, however, hardly allows such interpretation.

Indeterminate Family
Genus *Orhomalus* Etallon, 1861

Type species: *Orhomalus virgulinus* Etallon, 1861

Orhomalus deformis (Oppel, 1862)
Pl. XV (fig. 2)

1862 – *Magila deformis* Oppel; p. 49, Pl. 12 (fig. 4)
1925 – *Orhomalus deformis* (Oppel) *in* Van Straelen; p. 328
1929 – *Magila deformis* Oppel *in* Glaessner; p. 245
1929 – *Orhomalus deformis* (Oppel) *in* Glaessner; p. 281

Holotype by monotypy: BSPG AS VIII 115 (Oppel, 1862 – Pl. 12, fig. 4), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported one specimen, ascribed to this species, and housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS VIII 115 – Oppel (1862), Pl. 12 (fig.4) – incomplete specimen

Discussion. Oppel (1862) described this species on one incomplete specimen, ascribing it to *Magila* Münster, 1839, based upon the morphological characters of the chelae. However, Van Straelen (1925) pointed out that the shape of the chelae of pereiopod I is typical of *Orhomalus* Etallon, 1861. Even though the studied specimen is incomplete, it represents one of the most complete specimens of this genus since most species are based on isolate chelae.

Infraorder Palinura Latreille, 1803
Family Eryonidae De Haan, 1841
Genus *Cycleryon* Glaessner, 1965

Type species: *Macrourites propinquus* Schlotheim, 1822

Solnhofen species: *Cycleryon propinquus* (Schlotheim, 1822); *Cycleryon orbiculatus* (Münster, 1839); *Cycleryon elongatus* (Münster, 1839); *Cycleryon wulfi* Garassino & Schweigert, 2004

Cycleryon propinquus (Schlotheim, 1822) (♂)
Figs. 5, 6, 10, Pl. VI, Pl. XV (figs. 3, 4, 5, 6)

1822 – *Macrourites propinquus* Schlotheim; p. 35, Pl. 3 (fig. 2)
1825 – *Eryon Schlotheimi* König; p. 95, Pl. 8 (fig. 93)
1827 – *Eryon propinquus* (Schlotheim) *in* Germar; p. 99
1827 – *Eryon spinimanus* Germar; p. 99, **nov. syn.** (♀)
1829 – *Eryon Schlotheimi* König *in* Holl; p. 150
1836 – *Eryon Schuberti* v. Meyer; p. 271, Pl. 12 (figs. 3, 6), **nov. syn.**
1836 – *Eryon Schlotheimi* König *in* v. Meyer; p. 280
1838 – *Eryon Rehmanni* v. Meyer; p. 415
1836 – *Eryon speciosus* Münster; p. 5, Pl. 2, Pl. 3 (fig. 2)
1839 – *Eryon Meyeri* Münster; p. 6, Pl. 3 (fig. 1), Pl. 4
1839 – *Eryon Schuberti* v. Meyer *in* Münster; p. 13, Pl. 7 (figs. 6-9)
1839 – *Eryon elongatus* Münster; p. 9, Pl. 5 (fig. 7)
1852 – *Eryon propinquus* (Schlotheim) *in* Quenstedt; p. 267, Pl. 20 (fig. 19)
1853 – *Eryon propinquus* (Schlotheim) *in* Frischmann; p. 26
1853 – *Eryon speciosus* Münster *in* Frischmann; p. 26
1853 – *Eryon Schuberti* v. Meyer *in* Frischmann; p. 27
1855 – *Eryon propinquus* (Schlotheim) *in* Fraas; p. 92
1855 – *Eryon spinimanus* Germar *in* Fraas; p. 93
1856 – *Eryon spinimanus* Germar *in* v. Meyer; p. 44, Pl. 10 (fig. 1)
1857 – *Eryon spinimanus* Germar *in* Quenstedt; p. 805, Pl. 99 (figs. 26-27)
1857 – *Eryon speciosus* Münster *in* Quenstedt; p. 806, Pl. 90 (fig. 28, 31)
1862 – *Eryon propinquus* (Schlotheim) *in* Oppel; p. 12, Pl. 1 (figs. 2-4), Pl. 2 (fig. 1)
1862 – *Eryon spinimanus* Germar *in* Oppel; p. 13, Pl. 2 (fig. 2)
1862 – *Eryon Schuberti* v. Meyer *in* Oppel; p. 18, Pl. 3 (fig. 5)
1885 – *Eryon spinimanus* Germar *in* Quenstedt; p. 408, Pl. 32 (figs. 4-5)
1904 – *Eryon propinquus* (Schlotheim) *in* Peiser; p. 25
1904 – *Eryon propinquus* (Schlotheim) *in* Walther; p. 173
1907 – *Eryon propinquus* (Schlotheim) *in* v. Knebel; p. 213, Pl. 13
1908 – *Eryon propinquus* (Schlotheim) *in* Engel; p. 470
1822 – *Eryon propinquus* (Schlotheim) *in* Van Straelen; p. 1224
1825 – *Coleia propinqua* (Schlotheim) *in* Van Straelen; p. 148, Text-fig. 67
1904 – *Eryon spinimanus* Germar *in* Walther; p. 173
1904 – *Eryon Schuberti* v. Meyer *in* Walther; p. 173
1904 – *Eryon Schuberti* v. Meyer *in* Peiser; p. 34
1907 – *Eryon spinimanus* Germar *in* v. Knebel; p. 217, Text-fig. 1, Pl. 15
1907 – *Eryon Schuberti* v. Meyer *in* v. Knebel; p. 219
1908 – *Eryon spinimanus* Germar *in* Engel; p. 470
1924 – *Eryon propinquus* (Schlotheim) *in* Balss; p. 174, Figs. 1, 7
1925 – *Coleia spinimana* (Germar) *in* Van Straelen; p. 150, Pl. 5
1925 – *Knebelia Schuberti* (v. Meyer) *in* Van Straelen; p. 123
1928 – *Eryon propinquus* (Schlotheim) *in* Beurlen; p. 225
1929 – *Coleia propinqua* (Schlotheim) *in* Glaessner; p. 127

1929 – *Coleia spinimanus* (Germar) *in* Glaessner; p. 128
1929 – *Knebelia Schuberti* (v. Meyer) *in* Glaessner; p. 228
1930 – *Cyclocaris propinqua* (Schlotheim) *in* Beurlen & Glaessner; Text-fig. 12
1934 – *Eryon propinquus* (Schlotheim) *in* Dacqué; Pl. 42 (fig. 2)
1968 – *Eryon propinquus* (Schlotheim) *in* Leich; p. 90
1969 – *Cycleryon propinquus* (Schlotheim) *in* Glaessner; R 470, Text-fig. 274/4a, b
1969 – *Knebelia schuberti* (v. Meyer) *in* Malz; p. 296, Text-fig. 6
1969 – *Cycleryon propinquus* (Schlotheim) *in* Förster; p. 55, Pl. 3 (fig. 1)
1969 – *Cycleryon propinquus* (Schlotheim) *in* Malz; p. 293, Text-fig. 3
1978 – *Cycleryon propinquus* (Schlotheim) *in* Barthel; p. 328, 330, Pl. 44-45
1994 – *Cycleryon propinquus* (Schlotheim) *in* Frickhinger; p. 116, Figs. 197-198
1994 – *Cycleryon spinimanus* (Germar) *in* Frickhinger; Text-fig. 199
1994 – *Knebelia schuberti* (v. Meyer) *in* Frickhinger; p. 120, Fig. 210
1995 – *Cycleryon propinquus* (Schlotheim) *in* Dietl, Kapitzke & Rieter; Pl. 2 (fig. 2)
2000 – *Cycleryon propinquus* (Schlotheim) *in* Röper, Rothgaenger & Rothgaenger; Text-fig. 16
2001 – *Cycleryon spinimanus* (Germar) *in* Schweigert; p. 5, Text-fig. 1, Pl. 1 (figs. 1-2), Pl. 2 (figs. 1-2), Pl. 3 (figs. 1-4)
2001 – *Cycleryon spinimanus* (Germar) in Dietl & Schweigert; p. 108, Text-fig. 140

Diagnosis: carapace subcircular ventrally flattened; median postcervical carina strong and branchial carinae weak; cervical and postcervical incisions deep dividing margin into three parts; pereiopods I-IV chelate; pereiopod V achelate; pereiopod I larger and stronger than pereiopods II-V; pereiopods successively shorter posteriorly; uropodal exopod petaloid without diaeresis.

Lectotype: MNHB MB.A. 1107 (Schlotheim, 1822 – Pl. 3, fig. 2), housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Our studies revealed that *Eryon spinimanus* from Solnhofen and figured by Walch (1773 – Pl. 14, fig. 1) is synonym with *Cycleryon propinquus*, as discussed below. The original specimen is lost, so we decide to designate the specimen BSPG AS I 982 as the neotype (= allotype of *Cycleryon propinquus*) of Germar's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Our studies revealed that the minute *Eryon schuberti* from Solnhofen and figured by v. Meyer (1836 – Pl. 12, figs. 3, 6) is synonym with *Cycleryon propinquus*, as discussed below. This specimen, SMF X/m 144-146, is the holotype of v. Meyer's species, housed in Natur-Museum Senckenberg in Frankfurt am Main.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported 36 specimens belonging to this species, so divided: five from the Redenbacher collection, two from the Schlotheim collection, four from the Fraas collection and 25 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample two specimens of Schlotheim collection, housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, and three specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified one specimen, illustrated by Münster (1839), and two specimens, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 765 – Münster (1839), Pl. 3 (fig. 1) – length of the specimen: 10 cm

BSPG AS V 31 – Oppel (1862), Pl. 1 (fig. 2) – length of the specimen: 12 cm

BSPG AS VI 42 – Oppel (1862), Pl. 2 (fig. 1) – length of the specimen: 10 cm

Oppel (1862) reported four specimens which he assigned to *Cycleryon spinimanus* (Germar, 1827) so divided: one from the Alberti collection (today SMNS), one from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich and two from the Fraas collection (today SMNS). We studied two specimens of this original sample, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified one specimen, illustrated by Oppel (1862), and one specimen, illustrated by v. Knebel (1907). We report the list of the specimens, studied by Oppel and v. Knebel:

BSPG AS VI 40 – Oppel (1862), Pl. 2 (fig. 2) – length of the specimen: 12 cm

BSPG AS I 982 – Knebel (1907), Pl. 15 (fig. 1) – length of the specimen: 10 cm

Oppel (1862) reported 56 specimens which he assigned to *Eryon schuberti* v. Meyer, 1836, so divided: 16 from the Redenbacher collection and 40 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample four specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich illustrated by Münster (1839). We report the list of the specimens, studied by Münster:

BSPG AS VII 751 – Münster (1839), Pl. 7 (fig. 6) – length of the specimen: 2 cm

BSPG AS VII 755 – Münster (1839), Pl. 7 (fig. 2) – length of the specimen: 2 cm

BSPG AS VII 756 – Münster (1839), Pl. 7 (fig. 7) – incomplete specimen

BSPG AS VII 757 – Münster (1839), Pl. 7 (fig. 8) – length of the specimen: 1.5 cm

Description. Large eryonid with densely tuberculate exoskeleton.

Carapace. Carapace subcircular ventrally flattened, wider than long. Frontal margin strengthened with small tuburcles, without rostrum. Cervical and postcervical incisions deep dividing margin into three parts. Ocular incision small and narrow. Median postcervical carina strongly tuberculate. Branchial carinae weak and tuberculate. Posterior margin of carapace with row of strong tubercles. Lateral margins of carapace strongly dentate. Dorsal surface of carapace densely tuberculate.

Abdomen. Somite I subrectangular smaller than the others. Somites II-VI subrectangular of equal length. Pleurae and lateral parts of somites II-VI finely tubeculate, median part of somites smooth. Pleurae strongly dentate. Somites I-V with a strongly raised median tergal carina. Telson lanceolate with a strongly raised basal tubercle, a pair of proximal tubercles close to lateral margins, a median longitudinal carina, two submedian carinae, and rounded distal extremity. Protopod subsquare. Uropodal endopod subrectangular with a strong median longitudinal carina. Uropodal exopod petaloid without diaeresis and with a strong median longitudinal carina.

Cephalic appendages. Eyestalk very short. 3rd maxilliped elongate and spineless. Antennular articles thin of which the distal one carries two short multiarticulate flagella of equal length. Antennal articles short and stout of which the distal one carries a thin multiarticulate flagellum. Mouth field displaying crista dentata on 3rd maxilliped and mandibles (Fig. 5).

Fig. 5 – *Cycleryon propinquus* (Schlotheim, 1822), ventral view of carapace, line drawing (F. Fogliazza).

Thoracic appendages. Pereiopod I with strong and elongate propodus. Chela of pereiopod I with fixed finger gently curved in the distal part and movable finger curved distally with enlarged distal extremity. Thin median longitudinal carina extends for total length of propodus. Inner margins of movable and fixed fingers edentate in the male; three strong proximal teeth in the inner margin of movable finger in the female (Figs. 5, 6). Surface of merus, carpus, propodus, movable and fixed fingers smooth. Pereiopods II-IV with small chelae of equal length. Outer margins of carpus and propodus of pereiopods II-III strengthened with a row of small tubercles. Pereiopods V shorter than others and achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. Today, *Cycleryon* Glaessner, 1965, known from the Middle Jurassic (Callovian) to the Upper Jurassic (Tithonian) of Europe (France and Germany), includes five species. One from the Middle Jurassic, *C. giganteus* (Van Straelen, 1923) (France – Callovian); three from the Upper Jurassic (Kimmeridgian – Tithonian) of Germany, *C. propinquus* (Schlotheim, 1822), *C. elongatus* (Münster, 1839), and *C. orbiculatus* (Münster, 1839). *Cycleryon armatus* (v. Knebel, 1907) and *C. subrotundus* are interpreted as synonyms with *C. orbiculatus* (see *C. armatus* and *C. subrotundus* in this paper).

Recently, Garassino & Schweigert (2004) described from the Upper Jurassic (Tithonian) of Blumenberg quarry, close to the city of Eichstätt (Bavaria, S Germany), the new species *C. wulfi*.
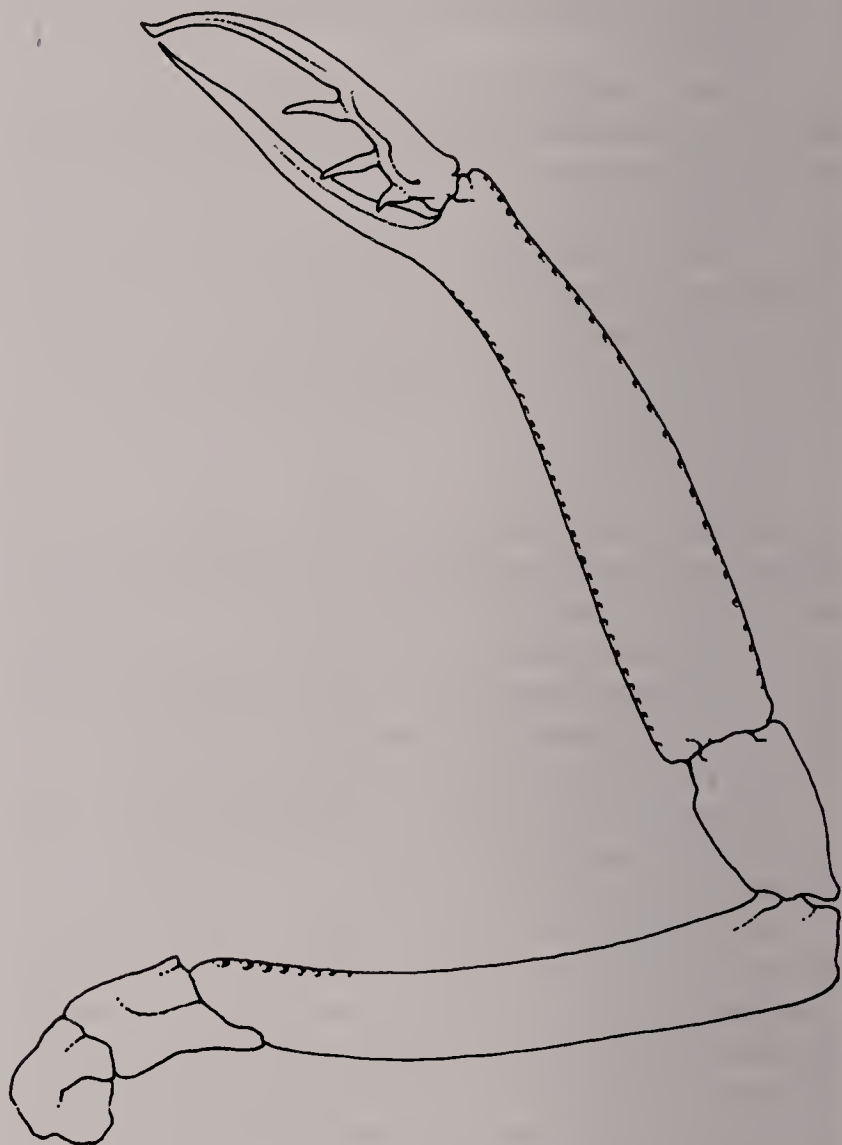
Fig. 6 – *Cycleryon spinimanus* (Germar, 1827), pereiopod I, line drawing (F. Fogliazza).

Germar (1827) pointed out that the presence of two strong spines in the proximal part of the inner margin of movable finger was a morphological character enough to distinguish *C. spinimanus* (Germar, 1827) from *C. propinquus* (Schlotheim, 1822). Subsequently, after the review of *Cycleryon* Glaessner, 1965, in the Nusplingen Lithographic Limestone (S Germany) by Schweigert (2001a), *C. spinimanus* is considered as the female of *C. propinquus*.

The poor state of preservation of the type specimen of *Eryon schuberti* v. Meyer, 1836, did not allow extending its morphological analysis. In fact, it is very difficult to recognize some diagnostic characters in order to describe this species, as already reported by Oppel (1862) who pointed out the poor preservation of the specimen. V. Meyer (1836) erected *E. schuberti* as new species of *Eryon* Desmarest, 1822. Van Straelen (1925)

ascribed this species to *Knebelia* Van Straelen, 1922, for the small size of its specimen with strongly curved chelae of perieopod I. Even though the original specimen shows the frontal margin with two subrectangular lobes typical of *Knebelia*, this morphological characters is also observable in many eryonid juvenile specimens belonging to *C. propinquus*. We consider the resemblace between *K. schuberti* and *K. bilobata*, type species of the genus, only a homoemorphy in order to consider the original specimen of *K. schuberti* as juvenile stage of *C. propinquus*.

Cycleryon orbiculatus (Münster, 1839)
Figs. 7a, 10, Pl. XVI (figs. 1, 2, 3, 4)

1839 – *Eryon orbiculatus* Münster; p. 7, Pl. 5 (figs. 1-2)
1839 – *Eryon latus* Münster; p. 8, Pl. 5 (figs. 4-6), Pl. 7 (fig. 1)
1839 – *Eryon subrotundus* Münster; p. 12, Pl. 7 (figs. 4-5), **nov. syn.**
1853 – *Eryon orbiculatus* Münster *in* Frischmann; p. 27
1853 – *Eryon latus* Münster *in* Frischmann; p. 27
1853 – *Eryon subrotundus* Münster *in* Frischmann; p. 27
1862 – *Eryon orbiculatus* Münster *in* Oppel; p. 14, Pl. 2 (fig. 3)
1862 – *Eryon subrotundus* Münster *in* Oppel; p. 14
1904 – *Eryon orbiculatus* Münster *in* Walther; p. 173
1907 – *Eryon orbiculatus* Münster *in* v. Knebel; p. 215
1907 – *Eryon armatus* v. Knebel; p. 215, Pl. 14, **nov. syn.**
1925 – *Coleia orbiculata* (Münster) *in* Van Straelen; p. 147
1925 – *Coleia armata* (Knebel) *in* Van Straelen; p. 153
1928 – *Eryon orbiculatus* Münster *in* Beurlen; p. 277
1929 – *Coleia orbiculata* (Münster) *in* Glaessner; p. 127
1929 – *Coleia armata* (Knebel) *in* Glaessner; p. 125
1994 – *Cycleryon orbiculatus* (Münster) *in* Frickhinger; p. 116, Fig. 196
2001 – *Cycleryon orbiculatus* (Münster) *in* Dietl & Schweigert; p. 54, Text.fig. 89

Diagnosis: carapace subcircular ventrally flattened; median postcervical carina, and branchial carinae absent; cervical and postcervical incisions deep dividing margin into three parts; suborbital tooth strong and outer orbital tooth strong; pereiopods I-IV chelate; pereiopod V achelate; pereiopod I larger and stronger than pereiopods II-V; pereiopods successively shorter posteriorly; uropodal exopod petaloid without diaeresis.

Lectotype: BSPG AS VII 760 – Münster (1839), Pl. 5 (fig. 2), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Our studies revealed that *Eryon armatus* from an unknown locality and figured by v. Knebel (1907 – Pl. 14) is synonym with *Cycleryon orbiculatus*, as discussed below. This specimen, MNHB MB.A. 236, is the lectotype of v. Knebel's species, housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Our studies revealed that *Eryon subrotundus* from Eichstätt and figured by Münster (1839 – Pl. 7, Fig. 5) is synonym with *Cycleryon orbiculatus*, as discussed below. This juvenile specimen, BSPG AS VII 762, is the lectotype of Münster's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – lower Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported 40 specimens belonging to this species, so divided: 15 from the Redenbacher collection, 24 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich and 1 from the Palaeontological Museum of Zurich (from Nusplingen). We studied three specimens of this original sample, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified three specimens, illustrated by Münster (1839), and one specimen, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VI 38 – Münster (1839), Pl. 7 (fig. 1) – length of the specimen: 8 cm

BSPG AS VII 760 – Münster (1839), Pl. 5 (fig. 2) – length of the specimen: 6 cm

BSPG AS I 990 – Oppel (1862), Pl. 2 (fig. 3) – length of the specimen: 5 cm

V. Knebel (1907) did not report in the description of *E. armatus* the number of studied specimens, illustrating only one specimen, today housed in the Museum für Naturkunde der Humboldt-Universität in Berlin:

MNHB MB.A. 236 – v. Knebel (1907), Pl. 14 – length of the specimen: 4 cm

Münster (1839) reported two specimens which he assigned to *Eryon subrotundus* Münster, 1839, belonging to the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, they are still preserved. We report the list of the specimens, studied by Münster:

BSPG AS VII 762 – Münster (1839), Pl. 7 (figs. 5) – length of the specimen: 3.5 cm

BSPG AS VII 763 – Münster (1839), Pl. 7 (fig. 4) – incomplete specimen

Description. Median-sized eryonid with densely tuberculate exoskeleton.

Carapace. Carapace subcircular ventrally flattened, wider than long. Frontal margin without rostrum. Cervical and postcervical incisions deep dividing margin into three parts. Ocular incision small and narrow. Suborbital tooth strong. Median postcervical and branchial carinae absent. Lateral margins of carapace strongly dentate. Dorsal surface of carapace densely tuberculate.

Abdomen. Somite I subrectangular smaller than the others. Somites II-VI subrectangular of equal length and with finely tubeculate dorsal surface. Pleurae finely tuberculate. Somites I-V with a weakly raised median tergal carina. Telson laceolate with a median longitudinal carina, two submedian carinae, and rounded distal extremity. Protopod subsquare. Uropodal endopod subrectangular with a strong median longitudinal carina. Uropodal exopod petaloid without diaeresis and with a strong median longitudinal carina.

Cephalic appendages. Eyestalk very short. 3rd maxilliped elongate and spineless. Antennular articles thin of which the distal one carries two short multiarticulate flagella of equal length. Antennal articles short and stout of which the distal one carries a thin multiarticulate flagellum.

Thoracic appendages. Pereiopod I with strong and stout propodus. Chela of pereiopod I with movable finger curved at distal extremity and straight fixed finger. Thin median longitudinal carina extends for total length of propodus. Inner margins of movable and fixed fingers edentate. Surface of merus, carpus, propodus, movable,

and fixed fingers smooth. Pereiopods II-IV with small chelae of equal length. Pereiopods V shorter than others and achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. Münster (1839) described this species on eight specimens, pointing out that they differed from the type species because the chela of pereiopod I was shorter and thicker. Today, only three original specimens are available and their study allowed recognition of other morphological characters useful to justify the systematic validity of this species. In fact, the strong suborbital tooth, the strong outer orbital tooth and the lack of carinae on the dorsal surface of carapace distinguish *C. orbiculatus* from the type species and from *C. elongatus* (see *C. elongatus* in this paper) (Fig. 7).
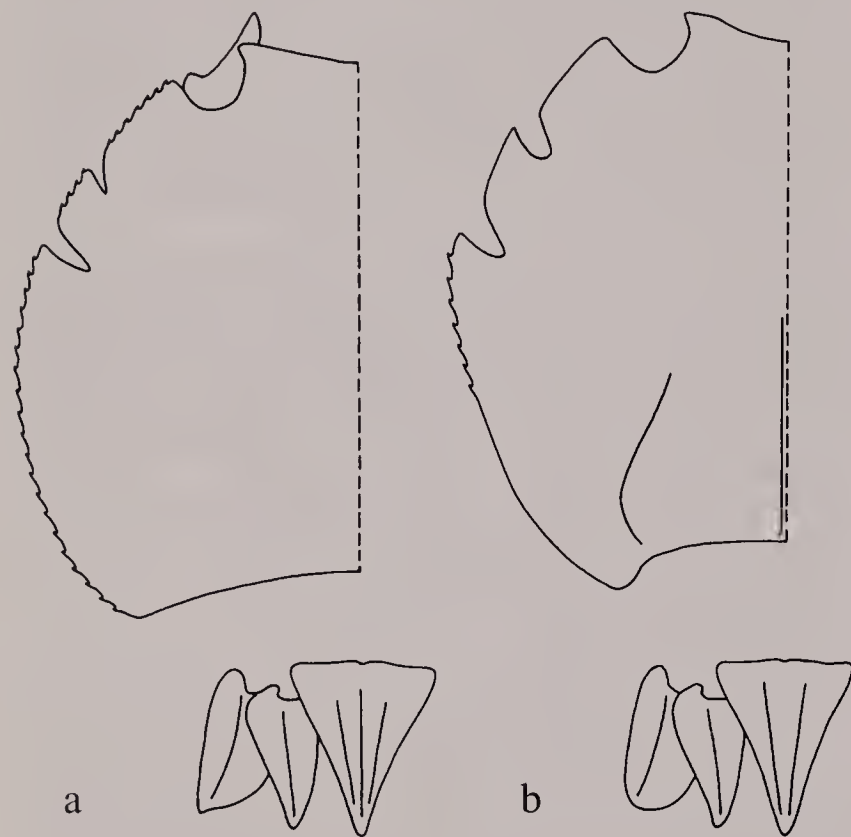
Fig. 7 – a) *Cycleryon orbiculatus* (Münster, 1839), line drawing; b) *Cycleryon elongatus* (Münster, 1839), line drawing (F. Fogliazza).

V. Knebel (1907) described *E. armatus* on some small-sized specimens, pointing out that they differed from *C. propinquus* and *C. orbiculatus* for the shorter chela of pereiopod I, the triangular shape of ocular incision, and the shorter abdomen. The study of the only available specimen allowed recognition of some morphological characters, typical of *C. orbiculatus* in order to consider the studied specimen as juvenile stage of this species. In fact, the shape of carapace wider than long, the strong suborbital tooth, the strong outer orbital tooth, and the lack of carinae on the dorsal surface of carapace are characters observable also in Münster's species.

Münster (1839) reported only some morphological characters of carapace and pereiopod I of *Eryon subrotundus* because the poor state of preservation of the specimens. Oppel (1862) pointed out that the original specimens studied by Münster could be juvenile stages of *C. orbiculatus*. This is confirmed by the re-study of the lectotype using ultraviolet illumination.

Cycleryon elongatus (Münster, 1839)
Figs. 7b, 10, Pl. XVI (fig. 5)

1839 – *Eryon elongatus* Münster; p. 9, Pl. 5 (fig. 7)
1853 – *Eryon elongatus* Münster *in* Frischmann; p. 27
1862 – *Eryon elongatus* Münster *in* Oppel; p. 15, Pl. 2 (fig. 4)
1904 – *Eryon elongatus* Münster *in* Walther; p. 173
1907 – *Eryon elongatus* Münster *in* v. Knebel; p. 216
1925 – *Coleia elongata* (Münster) *in* Van Straelen; p. 153
1929 – *Coleia elongata* (Münster) *in* Glaessner; p. 126
1969 – *Cycleryon elongatus* (Münster) *in* Malz; p. 295, Text-fig. 4
1999 – *Cycleryon elongatus* (Münster) *in* Frickhinger; p. 116, Fig. 195

Diagnosis: carapace subcircular ventrally flattened; median postcervical carina and branchial carinae weak; cervical and postcervical incisions deep dividing margin into three parts; pereiopods I-IV chelate; pereiopod V achelate; pereiopod I larger and stronger than pereiopods II-V; pereiopods successively shorter posteriorly; uropodal exopod rounded without diaeresis.

Lectotype: BSPG AS VII 761 (Münster, 1839 – Pl. 5, fig. 7), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported three specimens belonging to this species and housed in the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied this original sample recognizing one specimen, illustrated by Münster (1839), and two specimens, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 761 – Münster (1839), Pl. 5 (fig. 7) – length of the specimen: 8 cm

BSPG AS VI 43 – Oppel (1862), Pl. 2 (fig. 4) – length of the specimen: 8 cm

BSPG AS I 939 – Oppel (1862), Pl. 2 (fig. 4) – length of the specimen: 8 cm

One specimen (n. cat. 9419 – Wulf collection) was used to describe the carapace, poorly preserved in the original specimens.

Description. Median-sized eryonid with densely tuberculate exoskeleton.

Carapace. Carapace subcircular ventrally flattened, wider than long. Frontal margin without rostrum. Cervical and postcervical incisions deep dividing margin into three parts. Ocular incison small and narrow. Median postcervical carina weakly tuberculate and raised. Branchial carinae weak and tuberculate. Lateral margins of carapace weakly dentate. Dorsal surface of carapace densely tuberculate.

Abdomen. Somite I subrectangular smaller than the others. Somites II-VI subrectangular of equal length. Pleurae and lateral parts of somites II-VI finely tuberculate, median part of somites smooth. Pleurae weakly dentate. Somites I-V without a median tergal carina. Telson lanceolate with two submedian carinae and rounded distal extremity. Protopod subsquare. Uropodal endopod subrectangular with a strong median longitudinal carina. Uropodal exopod rounded without diaeresis and with a strong median longitudinal carina.

Cephalic appendages. Eyestalk very short. 3rd maxilliped elongate and spineless. Antennular articles thin of which the distal one carries two short multiarticulate

flagella of equal length. Antennal articles short and stout of which the distal one carries a thin multiarticulate flagellum. Mouth field displaying crista dentata on 3rd maxilliped and mandibles.

Thoracic appendages. Pereiopod I with strong, stout propodus. Chela of pereiopod I with movable finger curved at distal extremity and straight fixed finger. Thin median longitudinal carina runs for total length of propodus. Inner margins of movable and fixed fingers edentate. Surface of merus, carpus, propodus, movable, and fixed fingers smooth. Pereiopods II-IV with small chelae of equal length. Pereiopods V shorter than others and achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. Even though Münster (1839) did not establish the morphological characters, typical of this species, he pointed out that the short chela of pereiopod I was similar between *C. elongatus* and *C. orbiculatus*. Oppel (1862) compared *C. elongatus* with *C. propinquus*, telling that the sizes of pereiopod I and of the abdomen are different between the two species. In fact, pereiopod I is longer and the abdomen is smaller in the type species.

Even though there are some morphological affinities among *C. elongatus*, *C. orbiculatus,* and *C. propinquus*, the study of the original specimens revealed that the tail fan in *C. elongatus* is completely different than that on the other two. In fact, the telson in *C. elongatus* is characterized by only two lateral carinae, while in the other two species, the telson has one median longitudinal carina and two lateral carinae. Moreover, the uropodal exopod in *C. elongatus* has a rounded shape with rounded distal extremity, while in the other two species, the uropodal exopod has a petaloid shape with pointed distal extremity at the conjunction between the lower and lateral margins (Fig. 7).

Genus *Eryon* Desmarest, 1822

Type species: *Macrourites arctiformis* Schlotheim, 1822

Eryon arctiformis (Schlotheim, 1820)
Fig. 11, Pl. VII, Pl. XVII (fig. 1)

1820 – *Macrourites arctiformis* Schlotheim; p. 37
1822 – *Macrourites arctiformis* Schlotheim; p. 34, Pl. 3 (fig. 1)
1822 – *Eryon Cuvieri* Desmarest *in* Brogniart; p. 128, Pl. 10 (fig. 4)
1823 – *Eryon Cuvieri* Desmarest *in* Krüger; p. 587
1825 – *Eryon Cuvieri* Desmarest; p. 209, Pl. 34 (fig. 3)
1825 – *Eryon Cuvieri* Desmarest *in* Krüger; p. 265
1827 – *Eryon Cuvieri* Desmarest *in* Germar; p. 98
1827 – *Eryon acutus*? Germar; p. 100
1836 – *Eryon Cuvieri* Desmarest *in* v. Meyer; p. 273, Pl. 12 (fig. 5)
1837 – *Eryon arctiformis* (Schlotheim) *in* Bronn; p. 474, Pl. 137 (fig. 2)
1839 – *Eryon arctiformis* (Schlotheim) *in* Münster; p. 3, Pl. 1
1839 – *Eryon pentagonus* Münster; p. 10, Pl. 6 (fig. 1)
1839 – *Eryon subpentagonus* Münster; p. 10, Pl. 6 (fig. 2)
1862 – *Eryon arctiformis* (Schlotheim) *in* Oppel; p. 15, Pl. 3 (fig. 1)
1904 – *Eryon arctiformis* (Schlotheim) *in* Peiser; p. 25
1907 – *Eryon arctiformis* (Schlotheim) *in* v. Knebel: p. 200, Pl. 11 (fig. 1, 6), Pl. 12
1924 – *Eryon arctiformis* (Schlotheim) *in* Balss; p. 174, Text-figs. 3, 6
1925 – *Eryon arctiformis* (Schlotheim) *in* Van Straelen; p. 114, Text-fig. 63
1929 – *Eryon arctiformis* (Schlotheim) *in* Glaessner; p. 164
1969 – *Eryon arctiformis* (Schlotheim) *in* Glaessner; R 470, Text-fig. 274/2
1969 – *Eryon arctiformis* (Schlotheim) *in* Malz; p. 292, Text-figs. 1-2
1994 – *Eryon arctiformis* (Schlotheim) *in* Frickhinger; p. 120, Figs. 203-204
2005b – *Eryon arctiformis* (Schlotheim) *in* Schweigert & Garassino; p. 498

Diagnosis: carapace subcircular ventrally flattened; median postcervical carina and branchial carinae weak; cervical and postcervical incisions deep dividing margin into three parts; pereiopods I-IV chelate; pereiopod V achelate; pereiopod I larger and stronger than pereiopods II-V; pereiopods successively shorter posteriorly; uropodal exopod petaloid without diaeresis.

Holotype: *Macrourites arctiformis* (= *Eryon arctiformis*), MNHB K 38 MB.A. 253 (Schlotheim, 1822 – Pl. 3, fig. 1; length of the specimen: 7.5 cm), housed in the Museum für Naturkunde der Humboldt-Universität in Berlin.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported 170 specimens belonging to this species, so divided: 80 from the Redenbacher collection and 90 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample the holotype by Schlotheim, housed in the Museum für Naturkunde der Humboldt-Universität in Berlin, and six specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified five specimens, illustrated by Münster (1839), and one specimen, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 758 – Münster (1839), Pl. 2 – length of the specimen: 16 cm

BSPG AS VII 764 – Münster (1839), Pl. 1 (fig. 2) – length of the specimen: 11 cm

BSPG AS VII 766 – Münster (1839), Pl. 1 (fig. 3) – length of the specimen: 10 cm

BSPG AS VII 767 – Münster (1839), Pl. 1 (fig. 1) – length of the specimen: 12 cm

BSPG AS VII 1431 – Münster (1839), Pl. 6 (fig. 2) – length of the specimen: 7 cm

BSPG AS VI 41 – Oppel (1862), Pl. 3 (fig. 1) – length of the specimen: 10 cm

Description. Large eryonid with densely tuberculate exoskeleton.

Carapace. Carapace subcircular ventrally flattened, wider than long. Frontal margin strengthened with small tuburcles and without rostrum. Cervical and postcervical incisions deep dividing margin into three parts. Ocular incisions developed in conical structures carrying an elongate eyestalk. Median postcervical carina strongly tuberculate and raised. Branchial carinae weak and tuberculate. Posterior margin of carapace concave. Lateral margins of carapace strongly dentate, originally bearing fringes similar to those of *M. longimanatus* (not figured in the reconstruction). These fringed margins are only observable in

rapidly buried specimens, and they are not preserved in moults. Dorsal surface of carapace densely tuberculate.

Abdomen. Somite I subrectangular smaller than the others. Somites II-VI subrectangular of equal length and with finely tuberculate dorsal surface. Pleurae strongly dentate. Somites II-VI with a strongly raised median tergal carina. Telson lanceolate with a strongly raised median longitudinal carina and with pointed distal extremity. Protopod subsquare. Uropodal endopod subrectangular with a strong median longitudinal carina. Uropodal exopod petaloid without diaeresis and with a strong carina extending parallel to outer margin. In rapidly buried specimens, the uropodal endopod and exopod show a fringed margin.

Cephalic appendages. Eyestalk elongate. 3rd maxilliped elongate and spineless. Antennular articles thin of which the distal one carries two short multiarticulate flagella of equal length. Antennal articles short and stout of which the distal one carries a thin multiarticulate flagellum. Mouth field displaying crista dentata on 3rd maxilliped and mandibles.

Thoracic appendages. Pereiopod I with strong and elongate propodus. Chela of pereiopod I with fixed finger straight and movable finger bent distally with enlarged distal extremity. Inner margins of movable and fixed fingers edentate. Surface of merus, carpus, propodus, movable, and fixed fingers smooth. Pereiopods II-IV with small chelae of equal length. Pereiopods V shorter than others and achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. Today, *Eryon* Desmarest, 1822, known from the Middle Jurassic (Callovian) to the Upper Cretaceous (Campanian) of Europe (Germany, France and England), includes five species. Three from the Middle Jurassic: *E. perroni* Etallon, 1859, and *E. ellipticus* Van Straelen, 1922 (France – Callovian), and *E. sublevis* Carter, 1886 (England – Oxfordian). One from the Upper Jurassic: *E. arctiformis* (Schlotheim, 1822) (Germany – Kimmeridgian/Tithonian). One from the Lower Cretaceous: ?*E. neocomiensis* Woodward, 1881 (Silesia – Neocomian; inclusion in *Eryon* is very uncertain). *Eryon yehoachi* Remy & Avnimelech, 1955, from the Upper Cretaceous of Israel was redescribed as a fossil stomatopod species by Hof (1998).

Genus *Rosenfeldia* Garassino, Teruzzi & Dalla Vecchia, 1996

Type species: *Rosenfeldia triasica* Garassino, Teruzzi & Dalla Vecchia, 1996

Rosenfeldia oppeli (Woodward, 1866)
Pl. XVII (fig. 2)

1866 – *Eryon Oppeli* Woodward; p. 500, Pl. 24 (fig. 4)
1925 – *Eryon Oppeli* Woodward *in* v. Straelen; p. 120
1929 – *Eryon Oppeli* Woodward *in* Glaessner; p. 166
1963 – *Eryon oppeli* Woodward *in* Kuhn; p. 22
2003 – *Rosenfeldia oppeli* (Woodward) *in* Schweigert & Garassino; p. 178, Fig. 2A
2004a – *Rosenfeldia oppeli* (Woodward) *in* Schweigert, p. 70, Text-fig. without number
2004b – *Rosenfeldia oppeli* (Woodward) *in* Schweigert; p. 329, Text-fig. without number
2005a – *Rosenfeldia oppeli* (Woodward) *in* Schweigert & Frattigiani; p.198, Text-fig. without number
2005b – *Rosenfeldia oppeli* (Woodward) *in* Schweigert & Frattigiani; p. 328, Text-fig. without number

Holotype by monotypy: BM 44886, housed in the Natural History Museum in London.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: originally labelled as coming from Solnhofen. According to the lithology of the rock matrix it comes from the surroundings of Eichstätt.

Material: Woodward (1866) reported one incomplete specimen, belonging to the Häberlein collection and today housed in the Natural History Museum in London. In 2004 a second specimen was recovered from the Mörnsheim Formation of the Horstberg quarry near Mörnsheim (H. & K. Schumacher collection).

Discussion. Woodward (1866) based his description on an incomplete specimen belonging to the Häberlein collection, justifing the institution of *Eryon oppeli* on two morphological characters: pereiopod I is small if compared with the four succeding pereiopods and smaller than pereiopod I present in the other species of *Eryon* Desmarest, 1822, and the subrectangular telson exhibited rounded lateral margins that are different from the subtriangular telson typical of *Eryon*. Even though the poor state of preservation of the specimen did not allow recognition of the main morphological characters useful to establish its placement in this genus, surely the specimen must be ascribed to the family Eryonidae De Haan, 1841, for the lack of the diaeresis on the uropodal exopod.

Garassino *et al.* (1996) described *Rosenfeldia* from the Late Triassic (Norian) of NE Italy, belonging to the family Eryonidae for the lack of a diaeresis on the uropodal exopod and characterized by a subrounded carapace, chela of pereiopod I with movable finger longer than fixed finger and curved at the distal extremity, subrectangular telson with dentate lateral margins, and uropodal endopod and exopod with dentate lateral margins.

Even though the original specimen by Woodward is incomplete (only maxillae, pereiopods I-V, abdominal somites IV-VI and tail fan are preserved), its study pointed out some morphological characters, such as the dentate pleural margins of somites IV-VI, the dentate lateral margins of the telson and the dentate lateral margins of uropodal endopod and exopod, typical of *Rosenfeldia*. Therefore, *E. oppeli* is referred to this genus. In one of the newly recovered specimens (H. & K. Schumacher collection) the carapace is also missing, and its overall preservational state is worse than that of the holotype. Another two specimens (Frattigiani collection) exhibit also poor remains of the carapace (Schweigert, 2005; Schweigert & Garassino, in press). The ascription of *E. oppeli* to this genus expands the stratigraphic range of *Rosenfeldia*.

Rosenfeldia is now represented by two species, *R. triasica* (Norian) and *R. oppeli* (Tithonian). *Rosenfeldia* was only known by the type species *R. triasica* Garassino, Teruzzi & Dalla Vecchia, 1996, from the Upper Triassic (Norian) of NE Italy. *R. oppeli* differs from the Triassic one in bearing smaller chelae in pereiopod I, the lateral margins of pereiopods I-IV being smooth and the telson having a weak longitudinal median carina.

Genus *Knebelia* Van Straelen, 1922

Type species: *Eryon bilobatus* Münster, 1839

Knebelia bilobata (Münster, 1839)
Fig. 11, Pl. VIII, Pl. XVII (figs. 3, 4)

1839 – *Eryon bilobatus* Münster; p. 11, Pl. 6 (figs. 3-5)
1853 – *Eryon bilobatus* Münster *in* Frischmann; p. 27
1862 – *Eryon bilobatus* Münster *in* Oppel; p. 16, Pl. 3 (fig. 2)
1904 – *Eryon bilobatus* Münster *in* Peiser; p. 25, 32
1904 – *Eryon bilobatus* Münster *in* Walther; p. 173
1907 – *Münsteria bilobata* (Münster) *in* v. Knebel; p. 223
1922 – *Knebelia bilobata* (Münster) *in* Van Straelen; p. 982
1925 – *Knebelia bilobata* (Münster) *in* Van Straelen; p. 121
1929 – *Knebelia bilobata* (Münster) *in* Glaessner; p. 227
1969 – *Knebelia bilobata* (Münster) *in* Glaessner; R 470, Text-fig. 274/1
1994 – *Knebelia bilobata* (Münster) *in* Frickhinger; p. 120, Fig. 209

Diagnosis: carapace subsquare ventrally flattened; frontal margin with two subrectangular lobes and with a deep and very narrow cephalic incision; cervical and post-cervical incisions weak dividing margin into three parts; cervical groove weak; pereiopods I-IV chelate; pereiopod V achelate; pereiopod I larger and stronger than pereiopods II-V; pereiopods successively shorter posteriorly; uropodal exopod without diaeresis.

Lectotype: BSPG AS VI 39 (Oppel, 1862 – Pl. 3, fig. 2), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported ten specimens belonging to this species, so divided: four from the Redenbacher collection and six from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied four specimens of this original sample, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified three specimens illustrated by Münster (1839), and one specimen, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS VII 752 – Münster (1839), Pl. 6 (fig. 5) – length of the specimen: 3 cm

BSPG AS VII 753 – Münster (1839), Pl. 6 (fig. 4) – length of the specimen: 7 cm

BSPG AS VII 754 – Münster (1839), Pl. 6 (fig. 3) – length of the specimen: 7 cm

BSPG AS VI 39 – Oppel (1862), Pl. 3 (fig. 2) – length of the specimen: 8 cm

Description. Large eryonid with densely tuberculate exoskeleton.

Carapace. Carapace subsquare ventrally flattened. Frontal margin formed with two subrectangular lobes with a deep and very narrow cephalic incision and without rostrum. Cervical and postcerical incisions weak dividing margin into three parts. Ocular incision narrow located laterally. Cervical groove weak. Posterior margin narrow and strongly convex and strengthened by a row of small tubercles. Dorsal surface densely tuberculate.

Abdomen. Somite I subrectangular smaller than the others. Somites II-VI subrectangular of equal length and with finely tuberculate dorsal surface. Pleurae smooth. Somites II-VI with a median tergal carina strongly raised. Telson laceolate with one longitudinal median carina, two slightly raised submedian carinae, one basal tubercle, and pointed distal extremity. Protopod subsquare. Uropodal endopod subrectangular with a strong longitudinal median carina. Uropodal exopod subrectangular without diaeresis and with a strong longitudinal median carina.

Cephalic appendages. Eyestalk short. 3rd maxilliped, antennulae and antennae poorly preserved.

Thoracic appendages. Pereiopod I with slender and elongate propodus. Lower margin of merus with a row of small spines. Chela of pereiopod I with fixed finger straight and movable finger longer than fixed finger and bent distally with pointed distal extremity. Inner margins of movable and fixed fingers edentate. Surface of merus, carpus, propodus, movable, and fixed fingers smooth. Pereiopods II-IV with small chelae of equal length. Pereiopods V shorter than others and achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. Today, *Knebelia* Van Straelen, 1922, known only in the Upper Jurassic (Tithonian) of Germany, includes the only species, *K. bilobata* (Münster, 1839). *Eryon schuberti* v. Meyer, 1836, often included in *Knebelia*, represents a juvenile specimen of *Cycleryon propinquus* (Schlotheim, 1822).

Family Polychelidae Wood-Mason, 1874
Genus *Palaeopentacheles* v. Knebel, 1907

Type species: *Eryon roettenbacheri* Münster, 1839

Palaeopentacheles roettenbacheri (Münster, 1839)
Fig. 11, Pl. IX, Pl. XVII (fig. 5), Pl. XVIII (figs. 1, 2, 3, 4)

1839 – *Eryon Röttenbacheri* Münster; p. 13, Pl. 7 (fig. 10)
1848 – *Eryon Röttenbacheri* Münster *in* Bronn; p. 468
1852 – *Eryon Röttenbacheri* Münster *in* Quenstedt; p. 267
1853 – *Eryon Redenbacheri* Münster *in* Frischmann; p. 27
1856 – *Eryon Redenbacheri* Münster *in* v. Meyer; p. 49, Pl. 9 (figs. 1-3)
1862 – *Eryon Redenbacheri* Münster *in* Oppel; p. 18, Pl. 3 (figs. 6-7)
1904 – *Eryon Redenbacheri* Münster *in* Peiser; p. 43
1904 – *Eryon Redenbacheri* Münster *in* Walther; p. 173
1907 – *Palaeopentacheles Redenbacheri* (Münster) *in* v. Knebel; p. 226, Text-fig. 2
1924 – *Eryon Redenbacheri* Münster *in* Balss; p. 181, Text-fig. 9
1925 – *Palaeopentacheles Redenbacheri* (Münster) *in* Van Straelen; p. 124
1929 – *Palaeopentacheles Redenbacheri* (Münster) *in* Glaessner; p. 299
1969 – *Palaeopentacheles roettenbacheri* (Münster) *in* Glaessner; R 471, Text-fig. 275/2
1969 – *Palaeopentacheles redenbacheri* (Münster) *in* Malz; p. 298, Text-fig. 5
1969 – *Palaeopentacheles redenbacheri* (Münster) *in* Förster; p. 47
1994 – *Palaeopentacheles redenbacheri* (Münster) *in* Frickhinger; p. 122, Fig. 220
1994 – *Palaeopolycheles longipes* (Fraas) *in* Frickhinger; p. 122, Fig. 221
2001 – *Palaeopolycheles roettenbacheri* (Münster) *in* Dietl & Schweigert; p. 71
2005b – *Palaeopolycheles roettenbacheri* (Münster) *in* Schweigert & Garassino; p. 498

Diagnosis: carapace subrectangular ventrally flattened; projecting front having two strong and elongate teeth with serrate outer margins; lateral margins convex and denticulate; cervical groove well marked; median postcervical carina weak; branchial carinae strong; median postrostral carina weak; cervical and postcervical incisions absent; pereiopods I-IV chelate; pereiopod V achelate; pereiopod I larger and stronger than pereiopods II-V; pereiopods successively shorter posteriorly; uropodal exopod without diaeresis.

Lectotype: BSPG AS I 993 (Oppel, 1862 – Pl. 3, fig. 6), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported 20 specimens belonging to this species, so divided: six from the Redenbacher collection and 14 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied four specimens of this original sample, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified two specimens, illustrated by v. Meyer (1856) and two specimens, illustrated by Oppel (1862). We report the list of the specimens, studied by Meyer and Oppel:

BSPG AS I 991 – v. Meyer (1856), Pl. 9 (fig. 2) – incomplete specimen

BSPG AS I 992 – v. Meyer (1856), Pl. 9 (fig. 1) – length of the specimen: 5 cm

BSPG AS I 989 – Oppel (1862), Pl. 3 (fig. 7) – incomplete specimen

BSPG AS I 993 – Oppel (1862), Pl. 3 (fig. 6) – length of the specimen: 4 cm

Description. Small-sized eryonid with densely tuberculate exoskeleton.

Carapace. Carapace subrectangular ventrally flattened. Projecting front having two strong and elongate teeth with serrate outer margins. Cervical and postcervical incisions absent. Ocular incision deep located anteriorly. Cervical groove well marked. Median postcervical carina weak and tuberculate. Branchial carinae strong and tuberculate. Median postrostral carina weak. Lateral margins convex and denticulate. Posterior margin strongly convex. Dorsal surface densely tuberculate.

Abdomen. Somite I subrectangular smaller than the others. Somites II-VI subrectangular of equal length and with finely tuberculate dorsal surface. Pleurae pointed and tuberculate. Somites II-VI with a strongly raised median tergal carina, bearing a strong spine on each pleura directed backward. Somites II-V with a strong spine directed outward partially to cover each pleura. Telson laceolate with two submedian tuberculate carinae strongly raised, one strong basal spine, and tridentate distal extremity. Protopod subsquare. Uropodal endopod subrectangular with a strong longitudinal median carina. Uropodal exopod subrectangular with one small spine in the middle of the lateral margin and without diaeresis.

Cephalic appendages. Antennular articles thin of which the distal one carries two short multiarticulate flagella of equal length. Antennal articles short and stout of which the distal one carries a thin multiarticulate flagellum. Scaphocerite spatulate with a row of small spine along outer margin.

Thoracic appendages. Pereiopod I with slender and elongate merus with a row of small spines along the lower margin and strong propodus with upper and lower margins bearing small tubercles. Chela of pereiopod I with slender and pointed fixed finger and movable finger curved distally. Inner margins of movable and fixed fingers with strong teeth increasing in size distally. Surface of merus, carpus, propodus, movable, and fixed fingers tuberculate. Pereiopods II-IV with small chelae of equal length. Pereiopods V shorter than the others and achelate.

Abdominal appendages. Pleopods not preserved.

Discussion. V. Knebel (1907) established the new genus *Palaeopentacheles* with the type species *P. roettenbacheri* (Münster, 1839) from the Upper Jurassic (Tithonian) of Germany.

Recently, the discovery of *P. starri* by Schweitzer & Feldmann (2001) from the Oligocene of Washington (United States) largely expands the geographic and stratigraphic range of this genus.

Family Palinuridae Latreille, 1802
Genus *Palinurina* Münster, 1839

Type species: *Palinurina longipes* Münster, 1839

Included species: *Palinurina longipes* Münster, 1839; *Palinurina tenera* Oppel, 1862

Palinurina longipes Münster, 1839
Fig. 12, Pl. XVIII (fig. 5), Pl. IXX (fig. 1)

1839 – *Palinurina longipes* Münster; p. 37, Pl. 14 (fig. 8)

1839 – *Palinurina intermedia* Münster; p. 37, Pl. 14 (figs. 9,10?), Pl. 29 (Fig. 8), **nov. syn.**

1839 – *Palinurina pygmea* Münster; p. 38, Pl. 14 (fig. 11), **nov. syn.**

1862 – *Palinurina longipes* Münster *in* Oppel; p. 86, Pl. 24 (fig. 1)

1862 – *Palinurina pygmea* Münster *in* Oppel; p. 87, Pl. 24 (fig. 2)

1873 – *Palinurina longipes* Münster *in* Seebach; p. 345

1873 – *Palinurina tenera* Oppel *in* Seebach; p. 345

1889 – *Palinurina pygmea* Münster *in* Oppenheim; p. 718

1904 – *Palinurina longipes* Münster *in* Walther; p. 174

1904 – *Palinurina pygmea* Münster *in* Walther; p. 174

1925 – *Palinurina longipes* Münster *in* Van Straelen; p. 223

1929 – *Palinurina longipes* Münster *in* Glaessner; p. 301

1969 – *Palinurina longipes* Münster *in* Glaessner; R 474, Text-fig. 277/6

1973 – *Palinurina longipes* Münster *in* Förster; p. 38, Text-Figs. 4-7

1994 – *Palinurina longipes* Münster *in* Frickhinger; p. 125, Fig. 222

2001 – *Palinurina longipes* Münster *in* Dietl & Schweigert; p. 71

2005b – *Palinurina longipes* Münster *in* Schweigert & Garsssino; p. 498

Diagnosis: carapace subrectangular ventrally flattened; rostrum short, shorter than supraorbital spine; cervical and postcervical grooves deep; hepatic and branchiocardiac grooves thin and weak; supraorbital and antennal spines well developed; suborbital spine small; abdomen longer than carapace; pereiopod I shorter and stronger than pereiopods II-V; well-developed articles of the antennae; very elongate flagellum of antennae; uropodal exopod without diaeresis.

Lectotype: BSPG AS V 46 (Oppel, 1862 – Pl. 24, fig. 1), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Our studies revealed that *Palinurina intermedia* from Solnhofen and figured by Münster (1839 – Pl. 14, figs. 9-10) is synonym with *Palinurina longipes*, as discussed below. The specimen, BSPG AS VII 768, is the lectotype of Münster's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Our studies revealed that *Palinurina pygmea* from Solnhofen and figured by Münster (1839 – Pl. 14, fig. 11) is synonym with *Palinurina longipes*, as discussed below. This specimen, BSPG AS I 996, is the lectotype of Münster's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (upper Kimmeridgian – Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported 28 specimens belonging to this species, so divided: six from the Redenbacher collection and 22 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied two specimens of this original sample, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich in which we identified one specimen, illustrated by Münster (1839) and one specimen, illustrated by Oppel (1862). We report the list of the specimens, studied by Münster and Oppel:

BSPG AS V 47 – Münster (1839), Pl. 14 (fig. 8) – length of the specimen: 3 cm

BSPG AS V 46 – Oppel (1862), Pl. 24 (fig. 1) – length of the specimen: 4 cm

Münster (1839) reported a sample of three specimens which he assigned to *Palinurina intermedia*. We studied of this original sample two specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich illustrated by Münster (1839). We report the catalogue number of the two specimens, studied by Münster:

BSPG AS VII 767 – Münster (1839), Pl. 14 (fig. 10) – length of the specimen: 2 cm

BSPG AS VII 768 – Münster (1839), Pl. 14 (fig. 9) – length of the specimen: 3 cm

Oppel (1862) reported a sample of 48 specimens which he assigned to *Palinurina pygmea* Münster, 1839, so divided: 12 from the Redenbacher collection and 36 from the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We studied of this original sample one specimen, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich illustrated by Oppel (1862). We report the catalogue number of the specimen, studied by Oppel:

BSPG AS I 996 – Oppel (1862), Pl. 24 (fig. 2) – length of the specimen: 2 cm

One specimen (n. cat. 0315 – Wulf collection) was used to describe the carapace which was poorly preserved in the original sample.

Description. Small-sized palinurid with finely tuberculate exoskeleton.

Carapace. Carapace subrectangular ventrally flattened, something missing. Rostrum short, shorter than the supraorbital spines. A ridge of two/three spines directed forward the supraorbital spine. Antennal spine well developed, longer than the supraorbital spine. A ridge of three spines directed forward the antennal spine. Suborbital spine small, forming a ridge with other two small spines directed forward the ocular incision. Postcervical and cervical grooves deep. Hepatic and branchiocardiac grooves thin and weak. Two rows of small tubercles extend parallel on the median dorsal line of carapace, between the postcervical and branchiocardiac grooves.

Abdomen. Somites I-VI of equal length. Somites II-V with denticulated margins and with a sharp terminal spine. Tergal and pleural surfaces with small tubercles. Telson subrectangular with rounded distal extremity and with a short spine located in the median part of lateral margin. Uropodal endopod, exopod, and telson of equal length. Uropodal endopod and exopod with rigid and flexible portions. Uropodal exopod without diaeresis.

Cephalic appendages. Antennular articles thin of which the proximal one is longer than the other two. Antennal articles strong and stout with denticulate lateral margins. Antennal flagellum can exceed five time the length of the body.

Thoracic appendages. Pereiopod I shorter and stronger than pereiopods II-V. Segments of pereiopods I-V with small tubercles arranged in parallel rows.

Abdominal appendages. Pleopods with an unsegmented peduncle which carries two elongate multiarticulate flagella.

Discussion. *Palinurina* Münster, 1839, belongs to the family Palinuridae Latreille, 1802, known from the Upper Triassic with *Archaeopalinurus* Pinna, 1974, from the Norian of Cene (Bergamo, N Italy) (Pinna, 1974). Three genera belong to this family from the Jurassic: *Astacodes* Bell, 1863 (Germany, Slovakia – Kimmeridgian), *Palaeopalinurus* Bachmayer, 1954 (Germany – Tithonian), and *Palinurina* Münster, 1839 (England – Sinemurian/Toarcian; Germany – Tithonian). Five genera belong to this family from the Cretaceous: *Astacodes* Bell, 1863 (Europe, United States, Australia – Turonian/Santonian), *Eurycarpus* Schlüter, 1868 (Germany – Senonian), *Jasus* Parker, 1883 (Lebanon – Cenomanian), *Linuparus* White, 1847 (Germany, England, France, Canada, Antarctic Peninsula, United States, Mexico and New Zealand – Turonian/Campanian), and *Palinurus* Weber, 1795 (Italy – Albian; Germany, Lebanon – Turonian/Senonian). Finally, three genera belong to this family from the Cenozoic: *Archaeocarabus* McCoy, 1849 (England – Lutetian), *Jasus* Parker, 1883 (New Zealand – Oligocene), and *Justitia* Holthuis, 1946 (Italy – Lutetian).

Among the above mentioned genera, *Palinurina* Münster, 1839, strongly resembles, for the general shape of the body, *Archaeopalinurus*. However, if we examine more deeply the two forms, it is possible to point out some morphological differences that justify the separation into two different genera. If we compare our specimens with the reconstruction available in the litterature, particularly that concernig *A. levis* (Pinna, 1974 – Pl. 15, fig. 3; Garassino & Teruzzi, 1993 – Fig. 33) we can notice remarkable differences in the shape and in the ornamentation of the tail fan, in the length of pereiopods (the II and the IV are longer than the others in *A. levis*, while II-V have equal length in *P. longipes*), in the length of the antennal flagellum which is five time longer than the body in the German species. Other diagnostic differences appear to be seen in the morphology and ornamentation of the antennal peduncles and of the carapace, but the latter is too poorly preserved in *A. levis* to be sure about that.

Palinurina longipes Münster, 1839, was the subject of a review by Förster (1973). Today, *Palinurina*, known from the Sinemurian to the Tithonian (Lower-Upper

Jurassic) of Europe (England and Germany), includes two species, *P. longipes* and *P. tenera* (see next description).

Münter (1839) described *Palinurina intermedia* on some morphological characters different to those observed in the other species of the same genus, in particular *P. longipes*: the very elongate antennae are smooth, lacking the fine lateral setae, the large thick antennal stalk has three spiny articulations and all pereiopods are relatively shorter and thicker than those of the type species.

However Oppel (1862) reported that the specimens studied by Münster and labelled as *P. intermedia* were extremely poorly preserved and the general outline of the body and the pereiopods did not provide any differences with that of *P. longipes*, so considering Münster's species as synonym with the type species.

Münster (1839) described *Palinurina pygmea* on some morphological characters different to those observed in the other species of the same genus, in particular *P. longipes*: thinner and shorter antennae, shorter and more curved pereiopods and shorter abdomen. However, the study of the only survived specimen, belonging to this species, has pointed out some morphological characters, similar to those observed in *P. longipes* (cfr. description of *P. longipes*), such as shorter and stronger pereiopod I, segments of pereiopods I-V with small tubercles arranged in two parallel rows and antennal articles with small tubercles and spiny lateral margins. Therefore, we consider *P. pygmea* as synonym of *P. longipes*, type species of this genus on the basis of the above mentioned morphological characters, common between the two species. Probably, the specimens belonging to *P. pygmea*, gathered by Münster in the same species on the basis of the same size, were juvenile stages of *P. longipes*.

Palinurina tenera Oppel, 1862
Pl. IXX (figs. 2, 3)

1862 – *Palinurina tenera* Oppel; p. 86, Pl. 23 (fig. 4)
1873 – *Palinurina tenera* Oppel *in* Seebach; p. 345
1889 – *Palinurina tenera* Oppel *in* Oppenheim; p. 718
1904 – *Palinurina tenera* Oppel *in* Walther; p. 174
2005b – *Palinurina tenera* Oppel *in* Schweigert & Garassino; p. 498

The poor state of preservation of the original incomplete specimen by Oppel has led to the research of new specimens from private collections in order to emend the morphological description of *Palinurina tenera*. One specimen (n. cat. SMNS 65476 – Frattigiani collection) preserved in ventral view allowed recognition of some morphological characters in order to deepen the description of this species. However, the preservation in ventral view of Frattigiani's specimen did not permit description of the carapace and tail fan.

Diagnosis: abdomen longer than carapace; pereiopod I shorter and stronger than pereiopods II-V; articles of the antennae well developed; flagellum of antennae short; uropodal exopod without diaeresis.

Lectotype: BSPG AS I 995 (Oppel, 1862 – Pl. 23, fig. 4), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Eichstätt.

Material: Oppel (1862) reported 25 specimens belonging to this species and belonging to the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. We know of this original sample one specimen and illustrated by Oppel (1862). We report the catalogue number of the specimen, studied by Oppel:

BSPG AS I 995 – Oppel (1862), Pl. 23 (fig. 4) – incomplete specimen

Description. Small-sized palinurid with finely tuberculate exoskeleton.

Carapace. Not preserved.

Abdomen. Somites I-VI of equal length. Somites II-V with denticulated margins and with a sharp terminal spine. Tergal and pleural surfaces with small tubercles. Uropodal exopod without diaeresis.

Cephalic appendages. Antennular articles thin of which the proximal one is longer than the other two. Antennal articles strong and stout with smooth lateral margins. Antennal flagellum as long as the length of the body.

Thoracic appendages. Pereiopod I shorter and stronger than pereiopods II-V. Segments of pereiopods I-V with rare small tubercles not arranged in parallel rows.

Abdominal appendages. Not preserved.

Discussion. Oppel (1862) justified the difference of *P. tenera* from the type species based upon two morphological characters: the antennal flagellum which is shorter than that of *P. longipes* and the pereiopods that are longer than those of the type species. Even though it is difficult to compare the two species for their rarity, we are able to confirm the systematic validity of Oppel's species not only by the above-mentioned characters, but also for the antennal articles which have smooth lateral margins (denticulate in the type species) and for the segments of pereiopods I-V with rare small tubercles not arranged in parallel rows (many tubercles arranged instead in parallel rows in the type species).

Family Cancrinidae Beurlen, 1930
Genus *Cancrinos* Münster, 1839

Type species: *Cancrinos claviger* Münster, 1839

Cancrinos claviger Münster, 1839
Fig. 12, Pl. X, Pl. IXX (fig. 4), Pl. XX (figs. 1, 2, 3, 4, 5)

1839 – *Cancrinos claviger* Münster; p. 43, Pl. 15 (fig. 1)
1839 – *Cancrinos latipes* Münster; p. 44, Pl. 15 (fig. 2), **nov. syn.**
1862 – *Cancrinus claviger* Münster *in* Oppel; p. 88, Pl. 24 (fig. 3)
1862 – *Cancrinus latipes* Münster *in* Oppel; p. 88, Pl. 24 (fig. 4)
1904 – *Cancrinos claviger* Münster *in* Walther; p. 174
1904 – *Cancrinos latipes* Münster *in* Walther; p. 174
1925 – *Cancrinos claviger* Münster *in* Van Straelen; p. 226, Text-fig. 108
1929 – *Cancrinos claviger* Münster *in* Glaessner; p. 109
1929 – *Cancrinos latipes* Münster *in* Glaessner; p. 109
1969 – *Cancrinos claviger* Münster *in* Glaessner; R 475, Text-fig. 280/2
1994 – *Cancrinos claviger* Münster *in* Frickhinger; p. 115, Figs. 193-194
1999 – *Cancrinos claviger* Münster *in* Frickhinger; p. 42, Fig. 66
1999 – *Cancrinos latipes* Münster *in* Frickhinger; p. 42, Fig. 67
2006 – *Cancrinos claviger* Münster *in* Garassino & Schweigert; p. 75

This species is very rare in the lithographic limestone and usually the specimens are not well preserved. However, we were able to give its diagnosis and morphological description by the identification of some morphological characters of carapace, abdomen, pereiopods, and cephalic appendages in the original specimens of this species. Moreover, one specimen (BSPG 1975 IX 13) housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich was used to describe for the first time the shape of the abdominal somites and tail fan, not preserved in the original sample.

Diagnosis: carapace subrectangular ventrally flattened; rostrum absent; cervical groove deep; abdomen as long as carapace; pereiopod I shorter and stronger than pereiopods II-V; petaloid flagellum of the antennae strong and stout; uropodal exopod without diaeresis.

Neotype: BSPG AS I 998 (Oppel, 1862 – Pl. 24, figs. 5, 6), housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich. According to Münster (1839) the holotype was purchased by Prof. v. Breda from Leiden. Today the specimen seems to be lost, because it was not traceable either in the Teyler's Museum in Harlem, or in the British Natural History Museum in London, where specimens of v. Breda collection is said to be housed.

Our studies revealed that *Cancrinos latipes* from Moritzbrunn near Eichstätt and figured by Münster (1839 – Pl. 15, fig. 2) is synonym with *Cancrinos claviger*, as discussed below. This specimen, BSPG AS VII 769, is the holotype of Münster's species, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich.

Stratigraphic range: Upper Jurassic (Tithonian).

Type locality: Solnhofen.

Material: Oppel (1862) reported three specimens belonging to this species and belonging to the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, they are still preserved.

BSPG AS I 997 – Oppel (1862), Pl. 24 (fig. 3) – length of the specimen: 10 cm

BSPG AS I 998 – Oppel (1862), Pl. 24 (figs. 5, 6) – incomplete specimen

BSPG AS I 999 – Oppel (1862), Pl. 24 (fig. 4) – length of the specimen: 10 cm

Münster (1839) reported one specimen which he assigned to *Cancrinos latipes* Münster, 1839, belonging to the collection of the Bayerische Staatssammlung für Paläontologie und Geologie in Munich where, today, it is still preserved.

BSPG AS VII 769 – Münster (1839), Pl. 15 (fig. 2) – incomplete specimen

Description. Large palinurid with strongly tuberculate exoskeleton.

Carapace. Carapace subrectangular ventrally flattened. Rostrum absent. Cervical groove deep, located in the median part. Posterior margin strengthened by a thin marginal carina.

Abdomen. Somites I-VI subrectangular of equal length. Pointed pleurae with a strong, sharp tooth and denticulate margin. Telson subrectangular with rounded distal extremity. Uropodal endopod and exopod with rigid and flexible portions. Rigid portion of exopod finely tuberculate. Uropodal exopod without diaeresis.

Cephalic appendages. Antennular flagella thin and elongate. Antennal articles strong and stout with denticulate lateral margins. Antennal flagellum short and petaloid with 22 segments narrowing distally.

Thoracic appendages. Pereiopod I shorter and stronger than pereiopods II-V with a strong and stout dactylus. Upper and lower margins of I-V strengthened by a row of strong spines directed forward.

Abdominal appendages. Not preserved.

Discussion. Today, *Cancrinos* Münster, 1839, known only from the Upper Jurassic (Tithonian) of Germany includes just one species, *C. claviger*, very rare in the lithographic limestone. Recently, the new species *C. libanensis* has been recorded from the Cenomanian of Lebanon, extending the stratigraphic range of this genus (Garassino & Schweigert, 2006).

Oppel (1862), revising the two species distinguished by Münster (1839), *C. claviger* and *C. latipes*, used as diagnostic character the different number of segments of the antennal flagellum. In fact, the author pointed out that the antennal flagellum had 15 or 16 segments in *C. claviger*, while it had 18 segments in *C. latipes*. In reality, the study of the original specimens of the two species pointed out that the antennal flagellum exhibits the same number of segments (ca. 22 in all), as also confirmed by the study of new specimens, housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, in which the number of segments is included between 21 and 23, the exact number not easily countable because of the telescoping in the distal part of the flagellum. Moreover, the pereiopod I is shorter than the others in both species. Finally, we consider *C. claviger* as type species of *Cancrinos* because the most important diagnostic characters that identify the genus are preserved in the original specimens of this species.
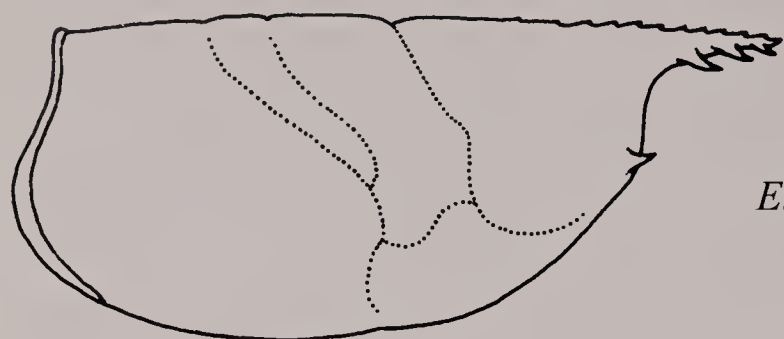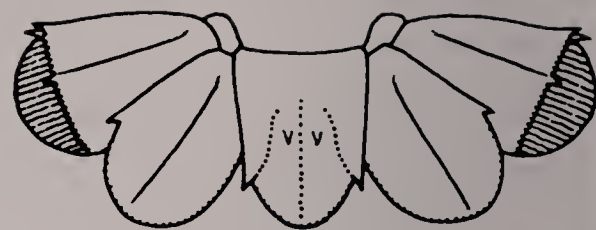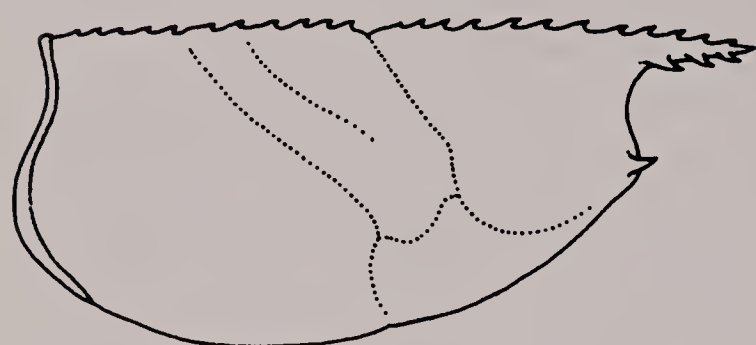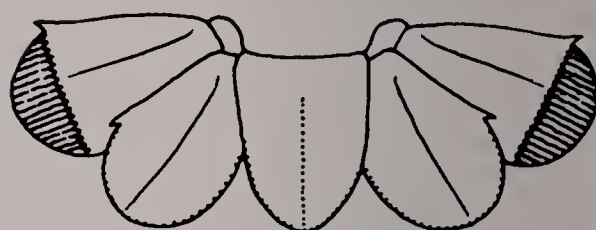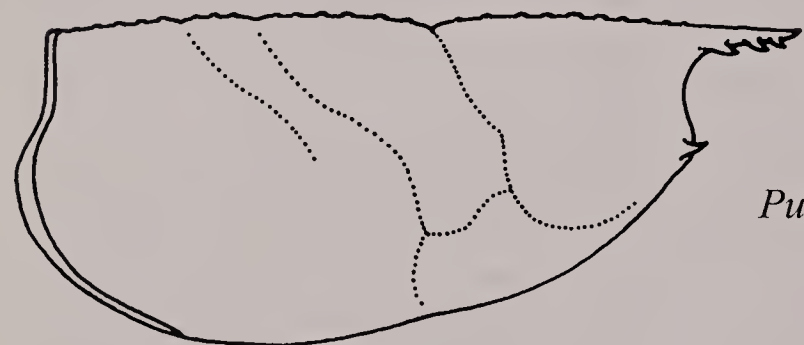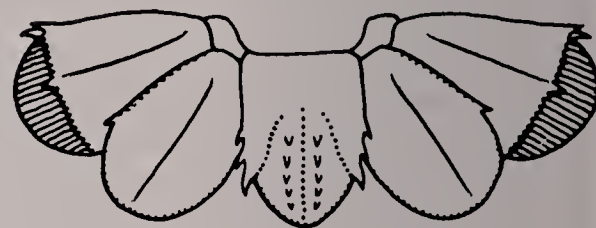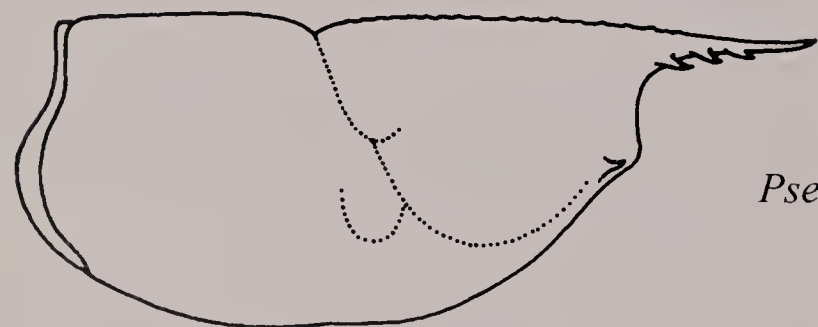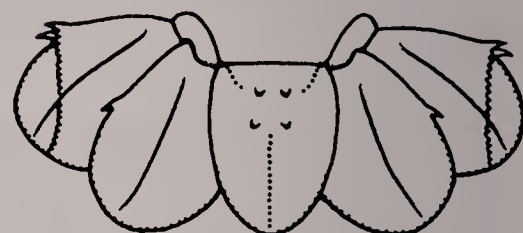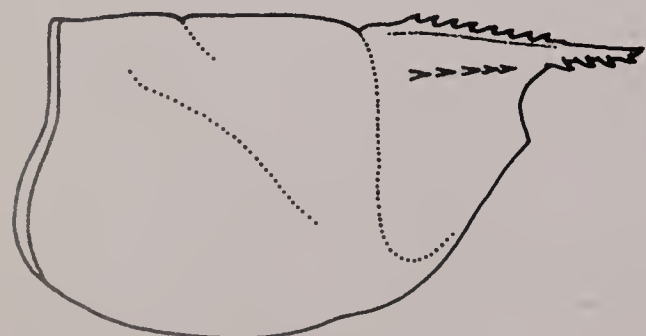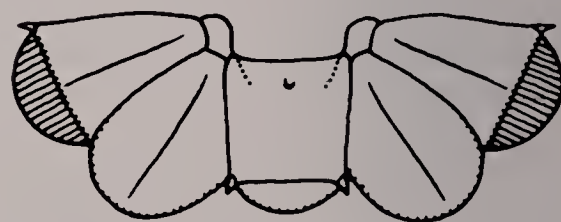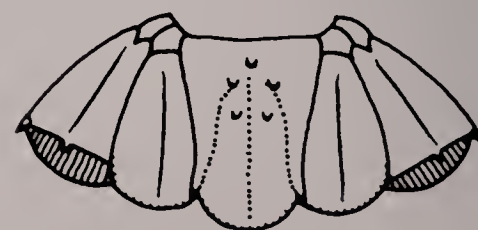
Fig. 8 – Summarizing figure of the astacideans preserved in Solnhofen fauna, line drawing (F. Fogliazza).
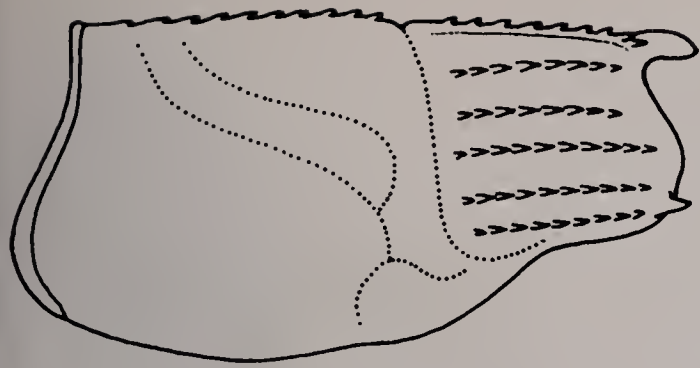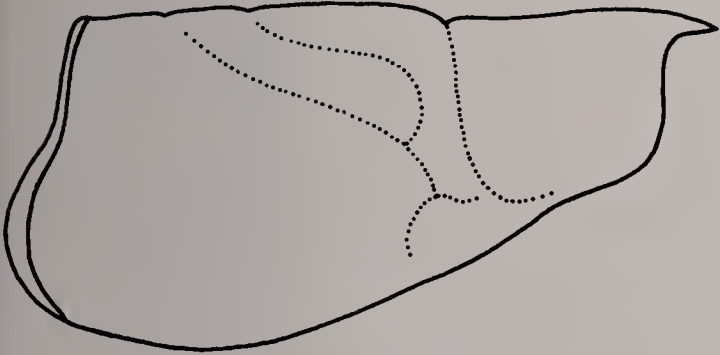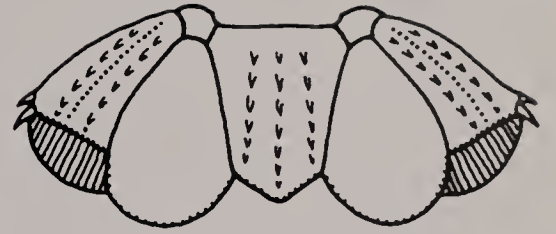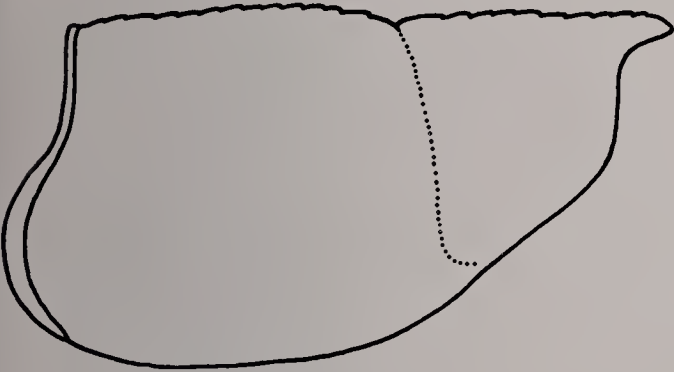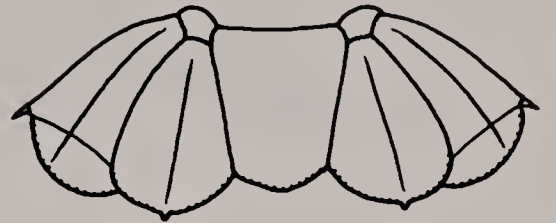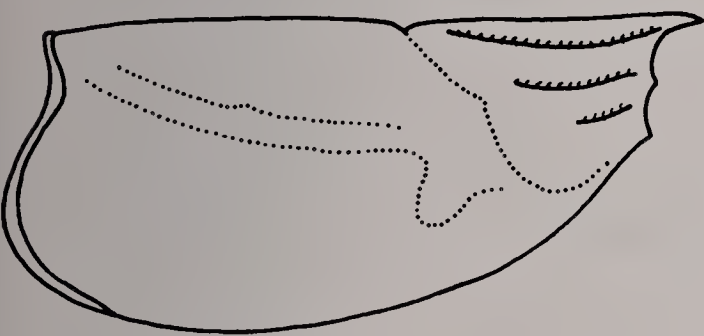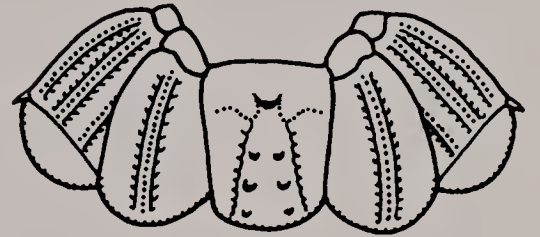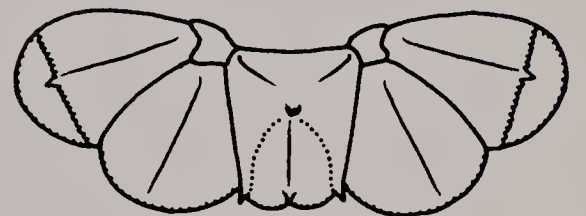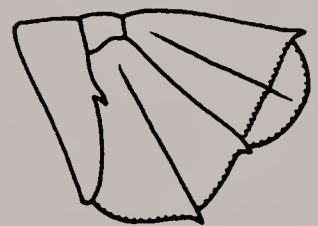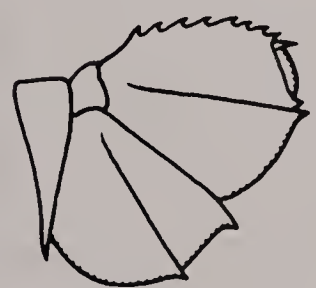
Fig. 9 – Summarizing figure of the astacideans and thalassinideans preserved in Solnhofen fauna, line drawing (F. Fogliazza).
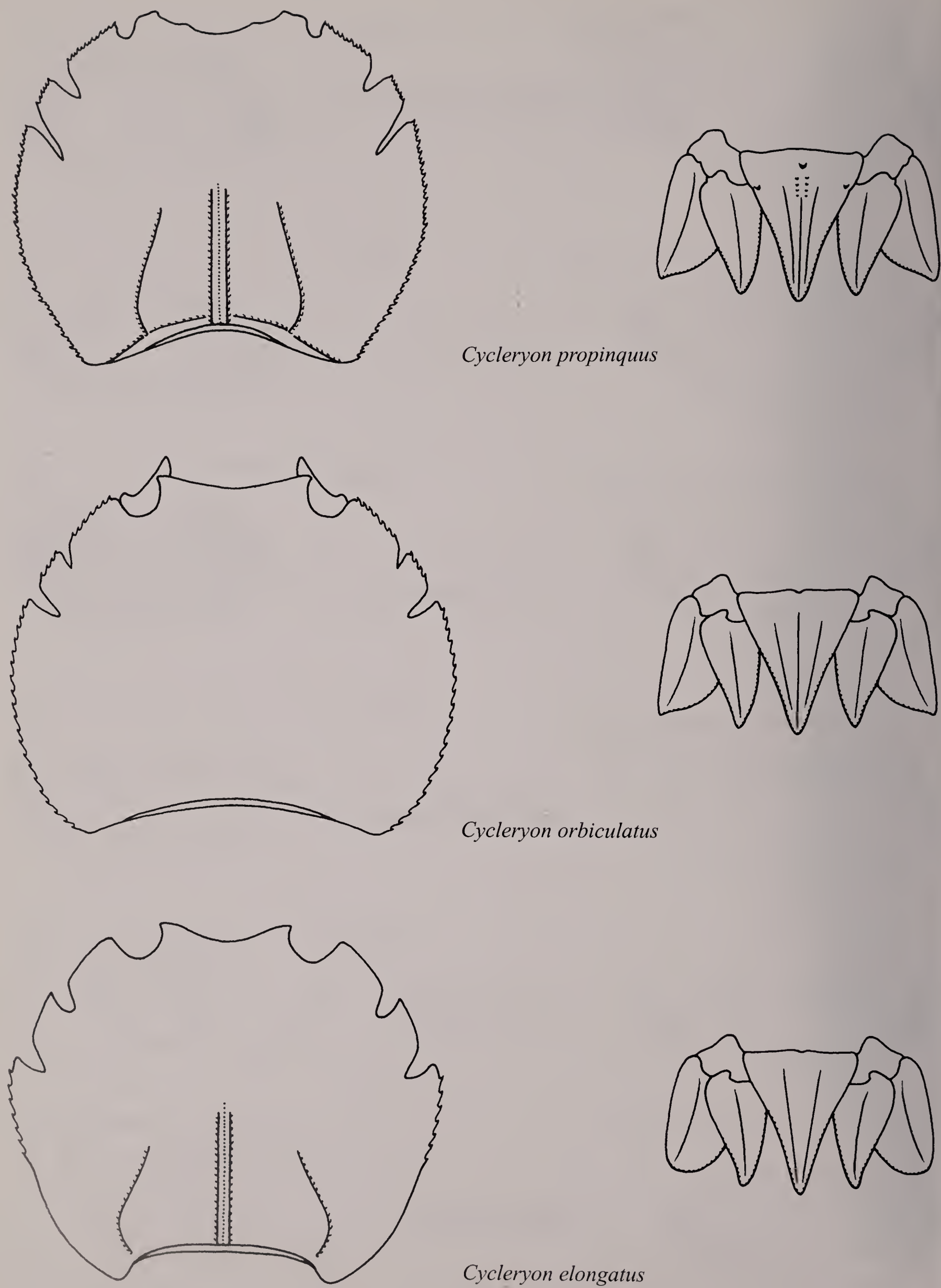
Fig. 10 – Summarizing figure of palinurids preserved in Solnhofen fauna, line drawing (F. Fogliazza).
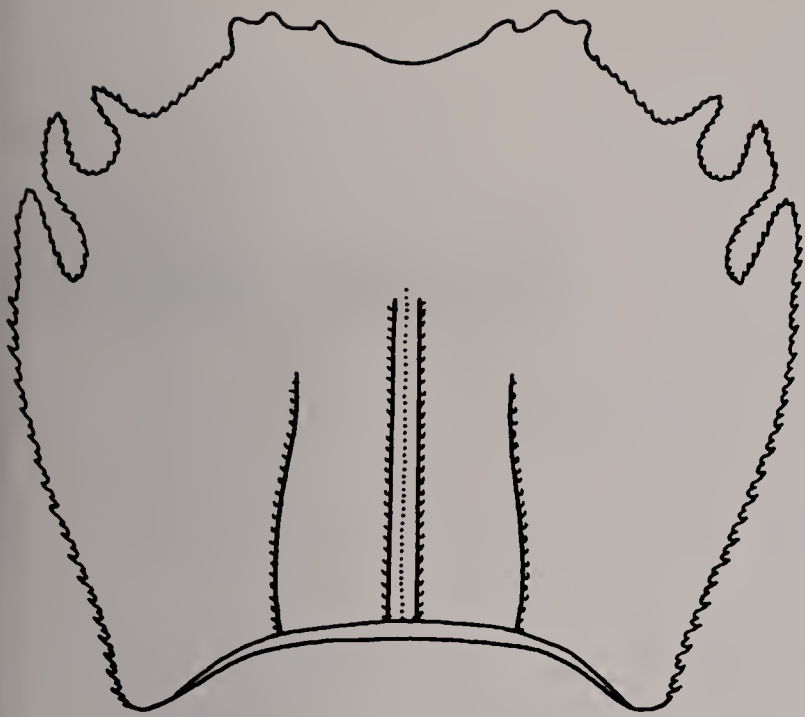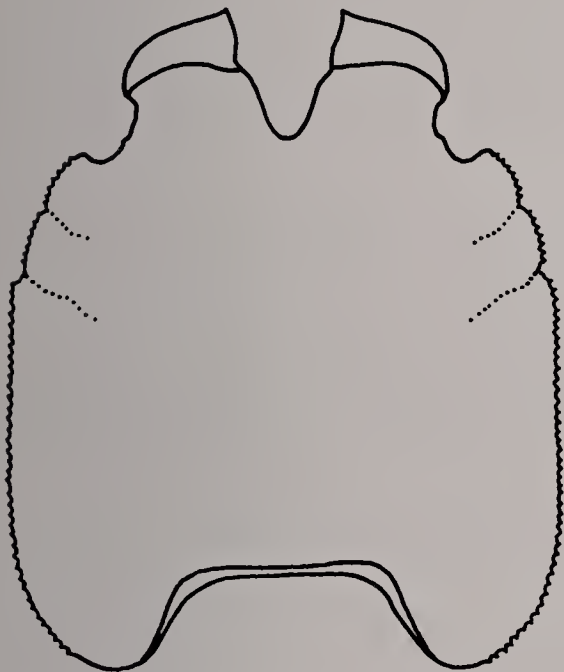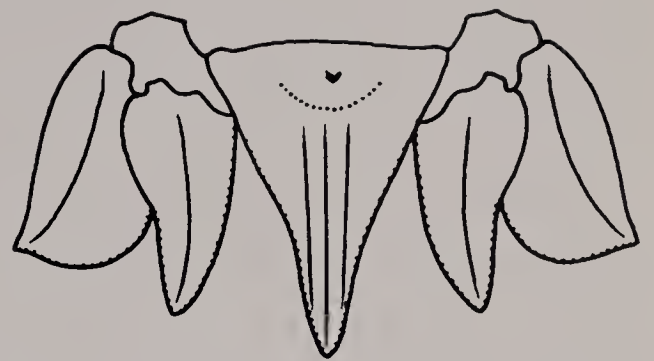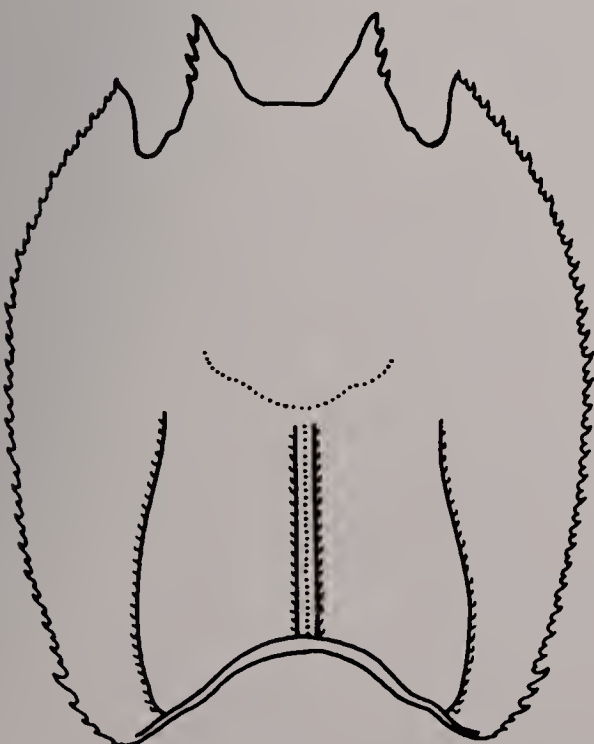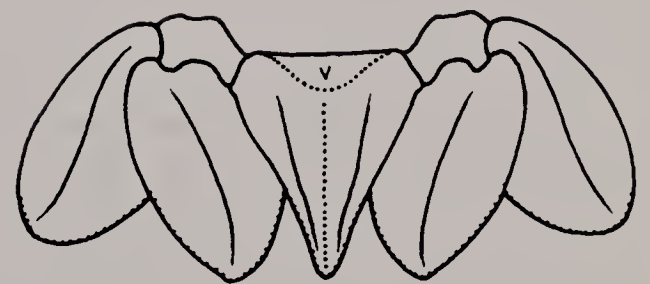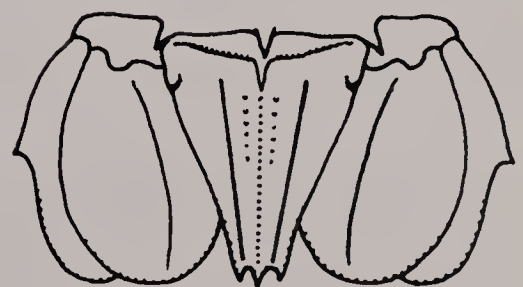
Fig. 11 – Summarizing figure of palinurids preserved in Solnhofen fauna, line drawing (F. Fogliazza).
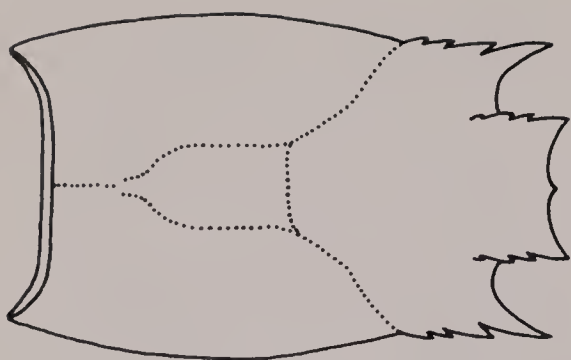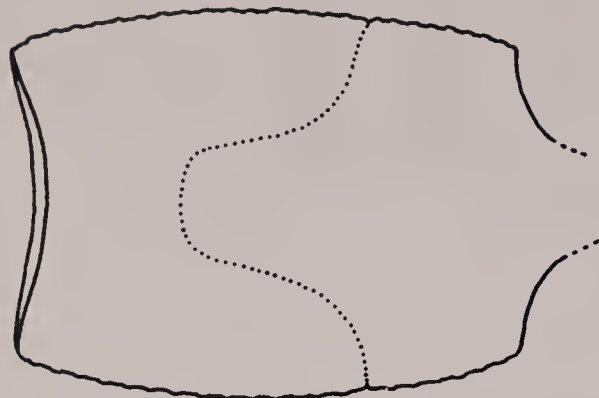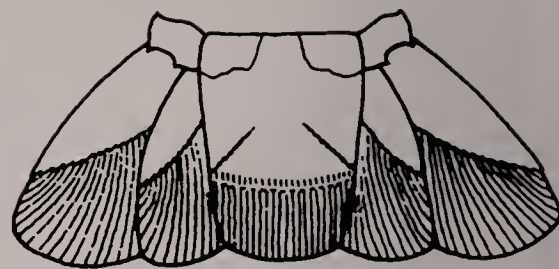
Fig. 12 – Summarizing figure of palinurids preserved in Solnhofen fauna, line drawing (F. Fogliazza).

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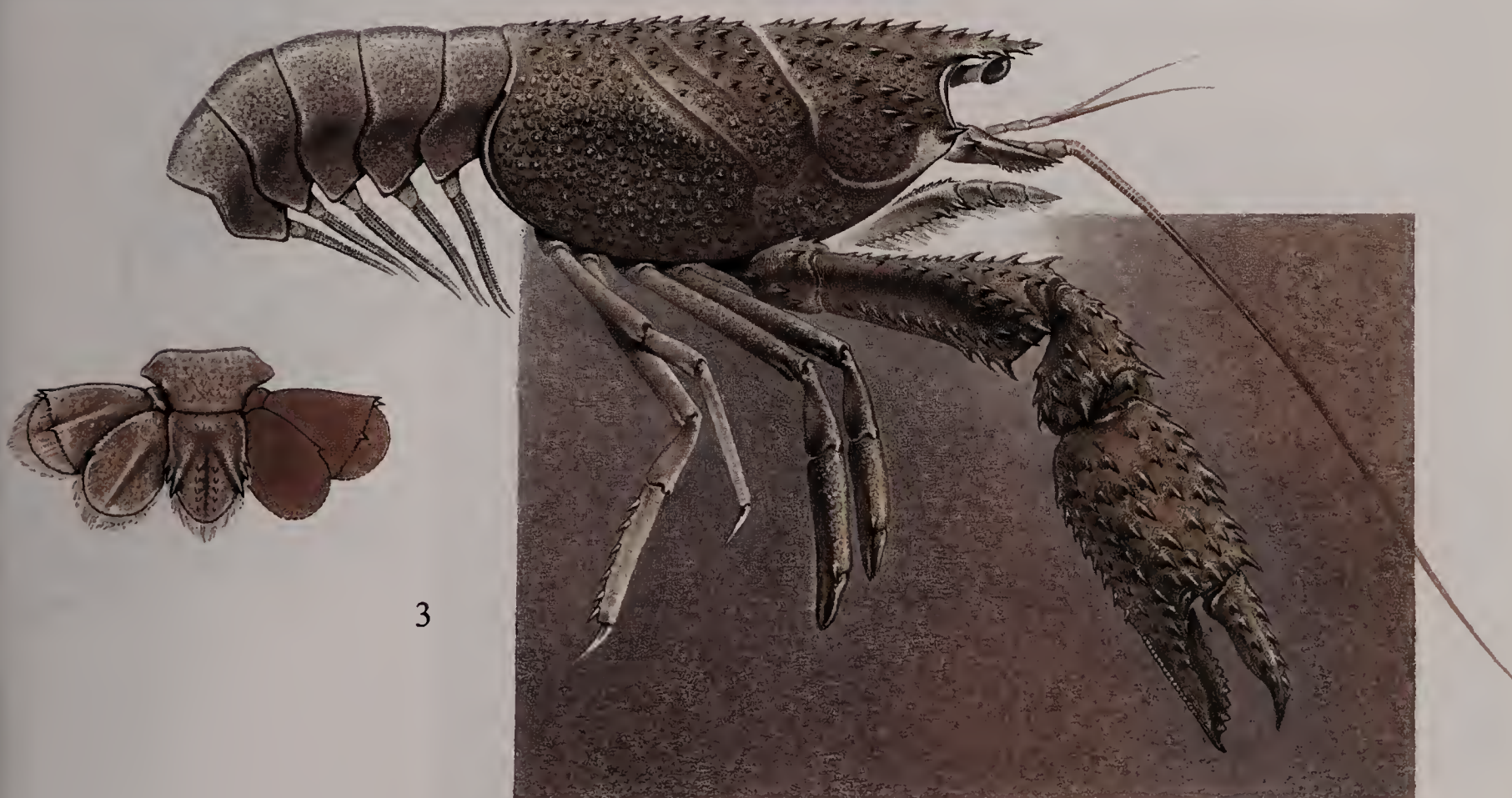
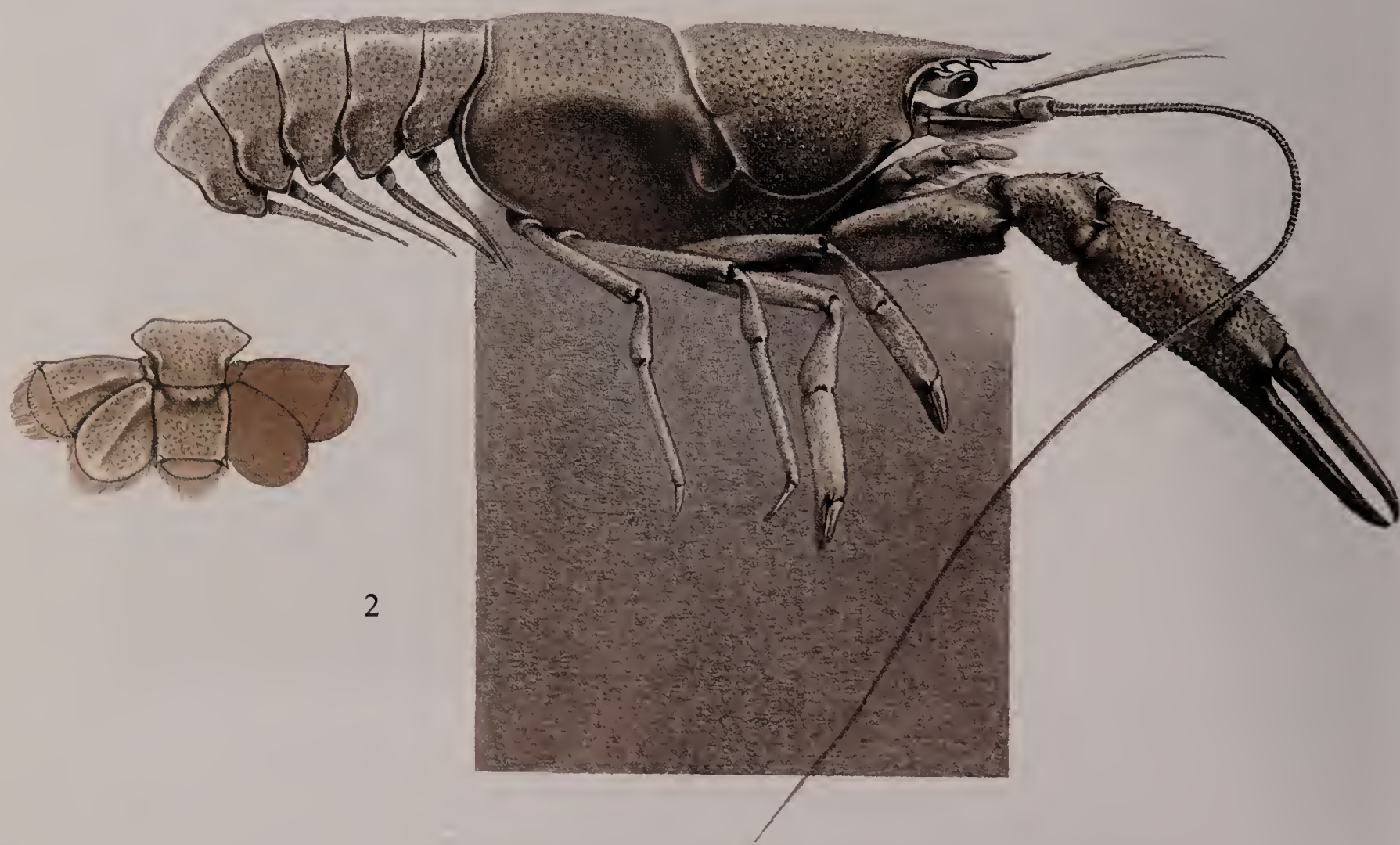
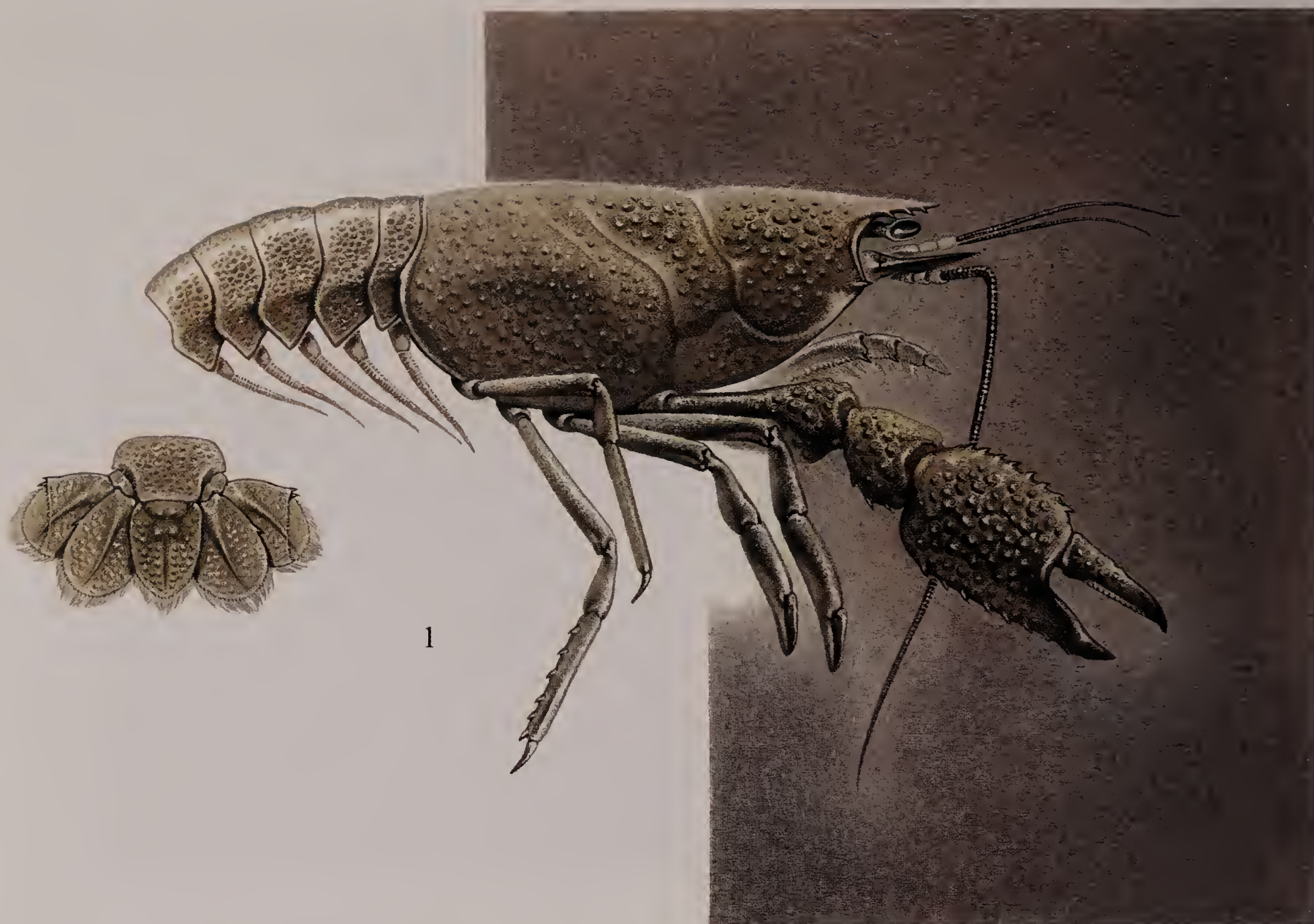
The Upper Jurassic Solnhofen decapod crustacean fauna: review of the types from old descriptions. Part I.
Infraorders Astacidea, Thalassinidea, and Palinura
Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano
Volume XXXIV – Fascicolo I

Pl. I – 1) *Eryma modestiforme* (Schlotheim, 1822); 2) *Eryma veltheimii* (Münster, 1839); 3) *Palaeastacus fuciformis* (Schlotheim, 1822). Reconstructions F. Fogliazza.

Pl. II – 1) *Pustulina minuta* (Schlotheim, 1822); 2) *Pseudastacus pustulosus* (Münster, 1839). Reconstructions F. Fogliazza.

Pl. III – 1) *Stenochirus angustus* (Münster, 1839); 2) *Glyphea pseudoscyllarus* (Schlotheim, 1822). Reconstructions F. Fogliazza.

Pl. IV – 1) *Glyphea tenuis* Oppel, 1860; 2) *Squamosoglyphea squamosa* (Münster, 1839). Reconstructions F. Fogliazza.

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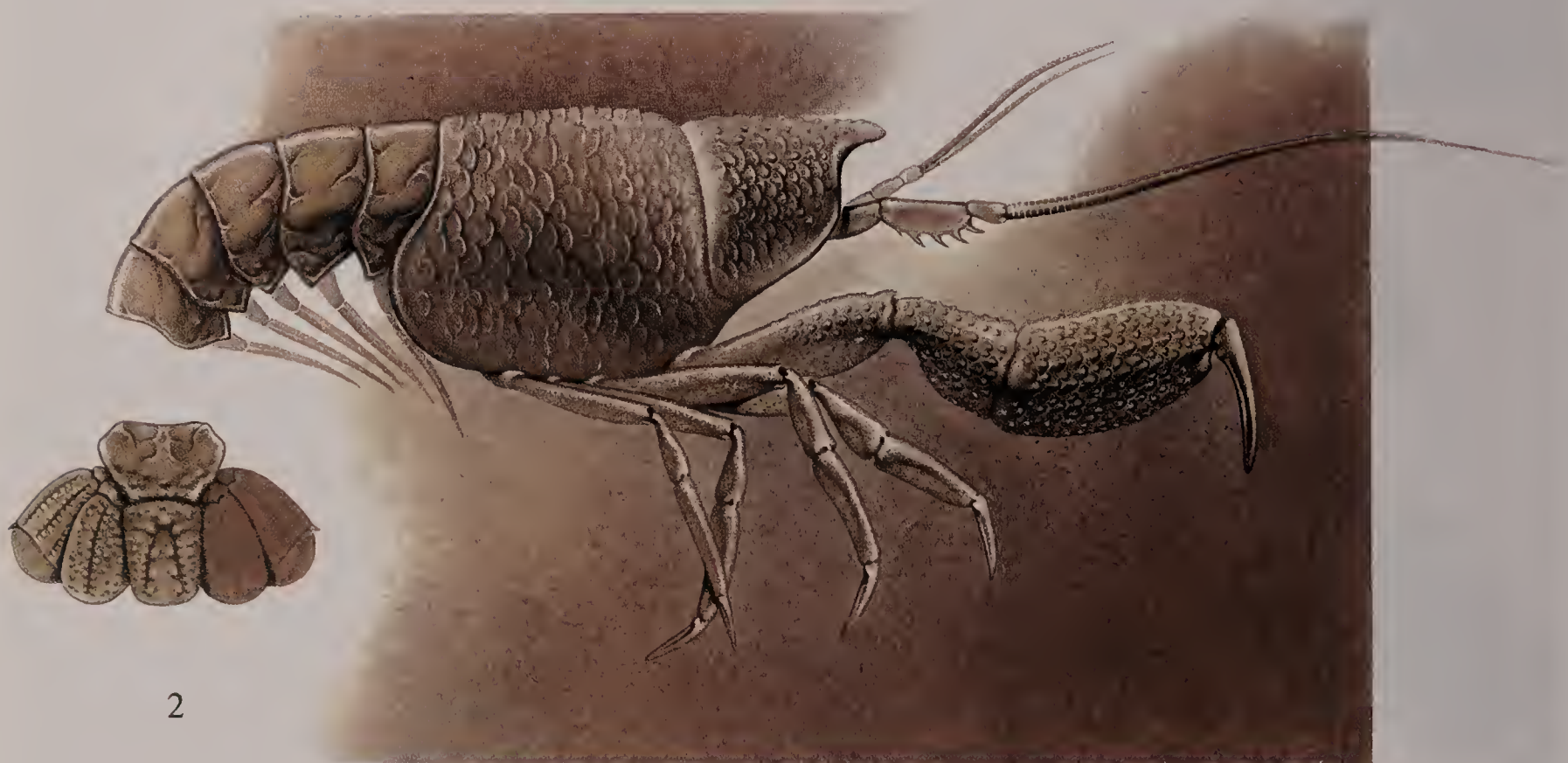
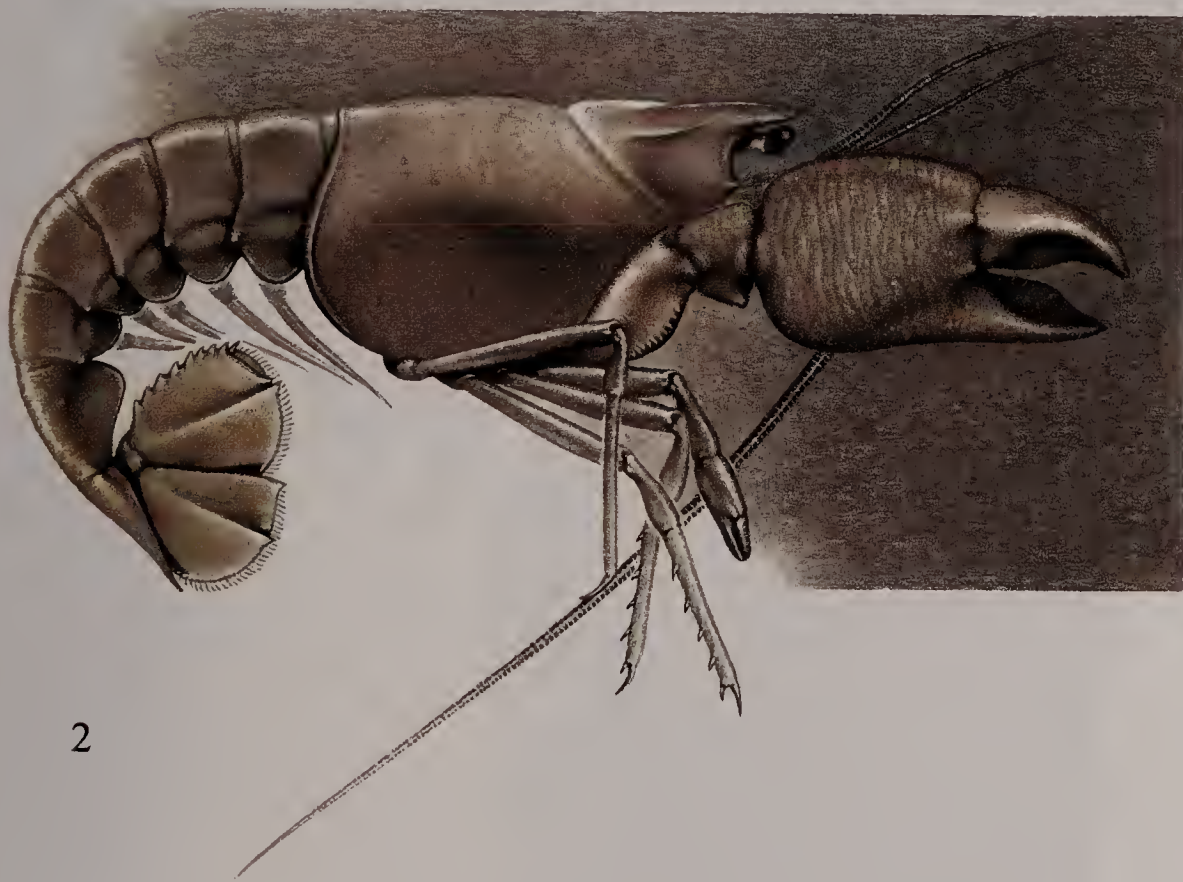
Pl. V – 1) *Mecochirus longimanatus* (Schlotheim, 1822); 2) *Magila latimana* Münster, 1839. Reconstructions F. Fogliazza.

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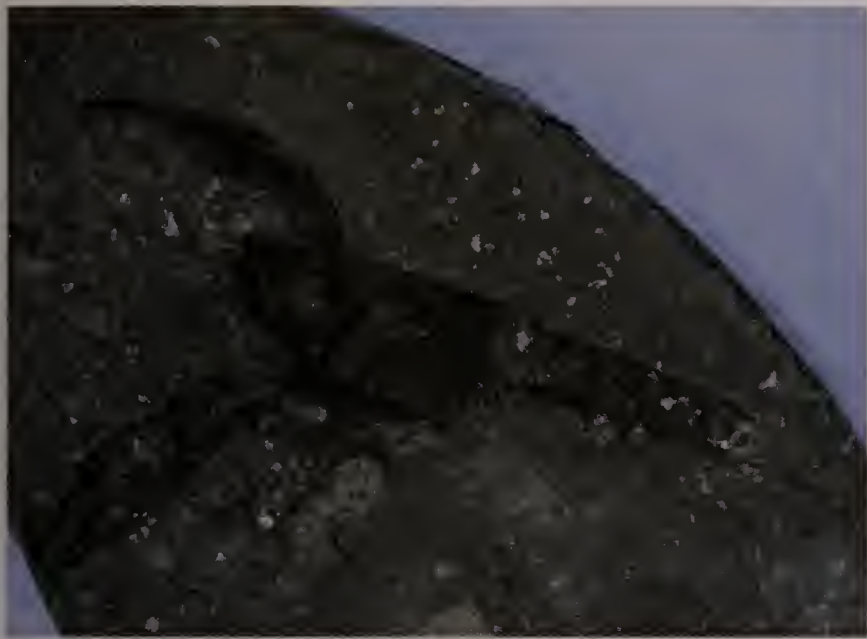
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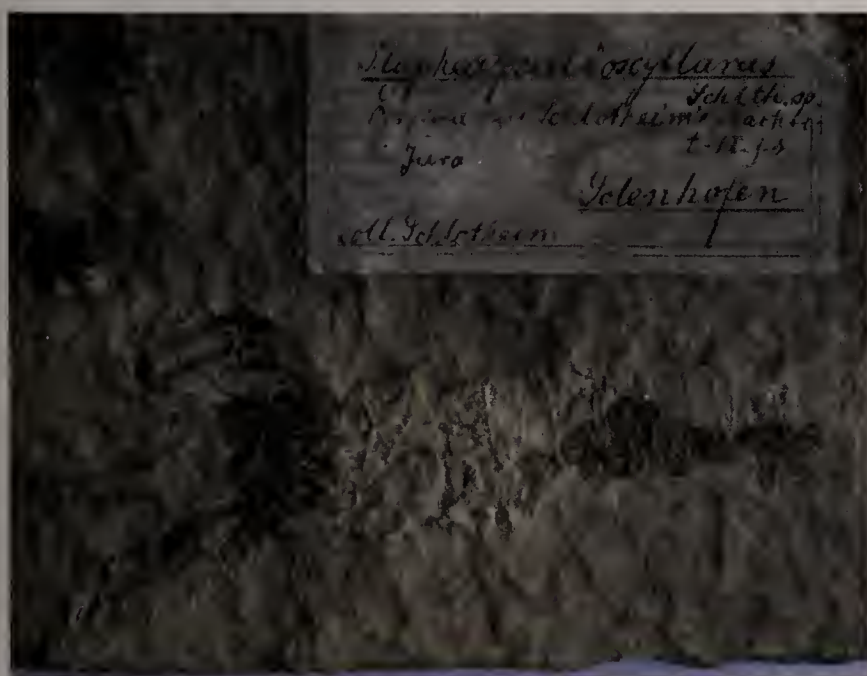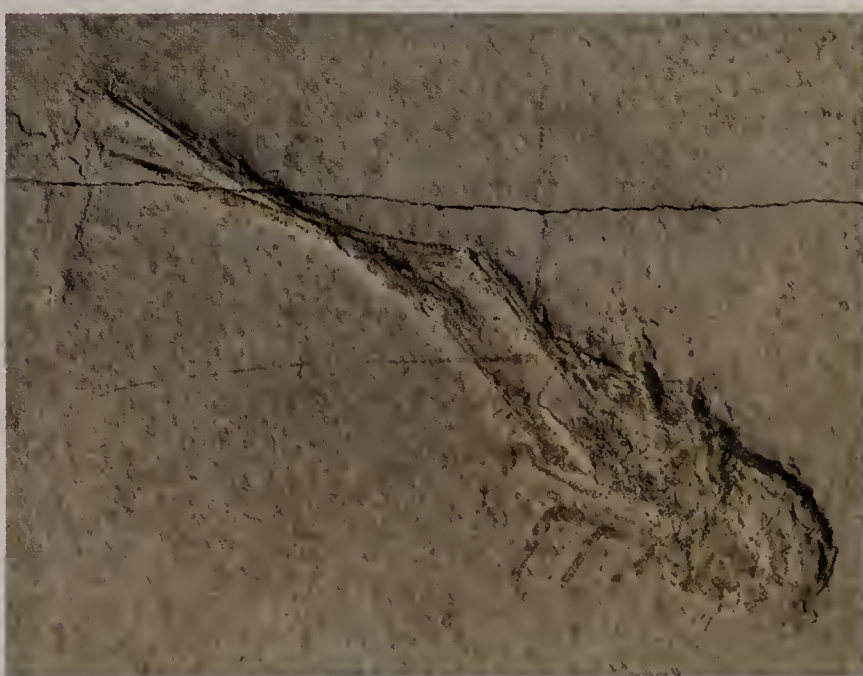
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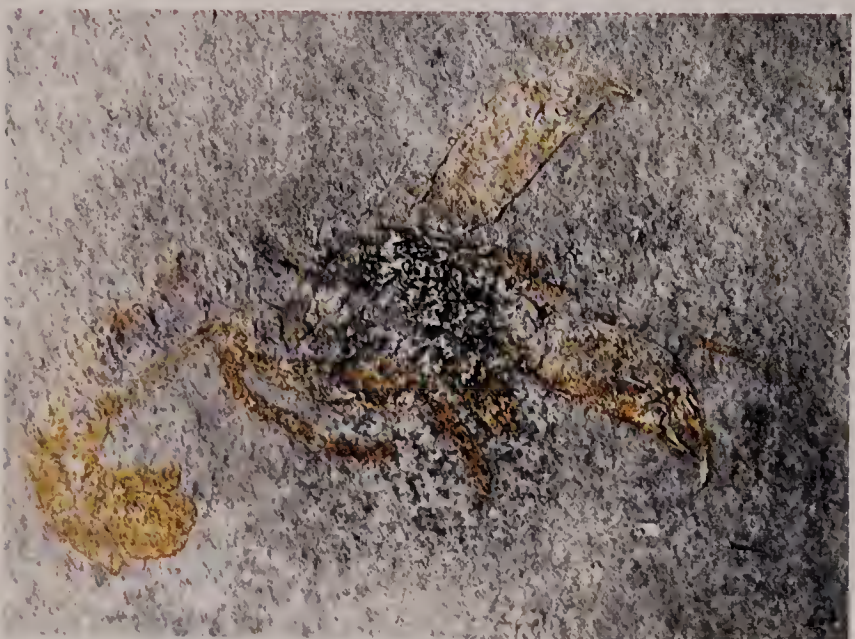
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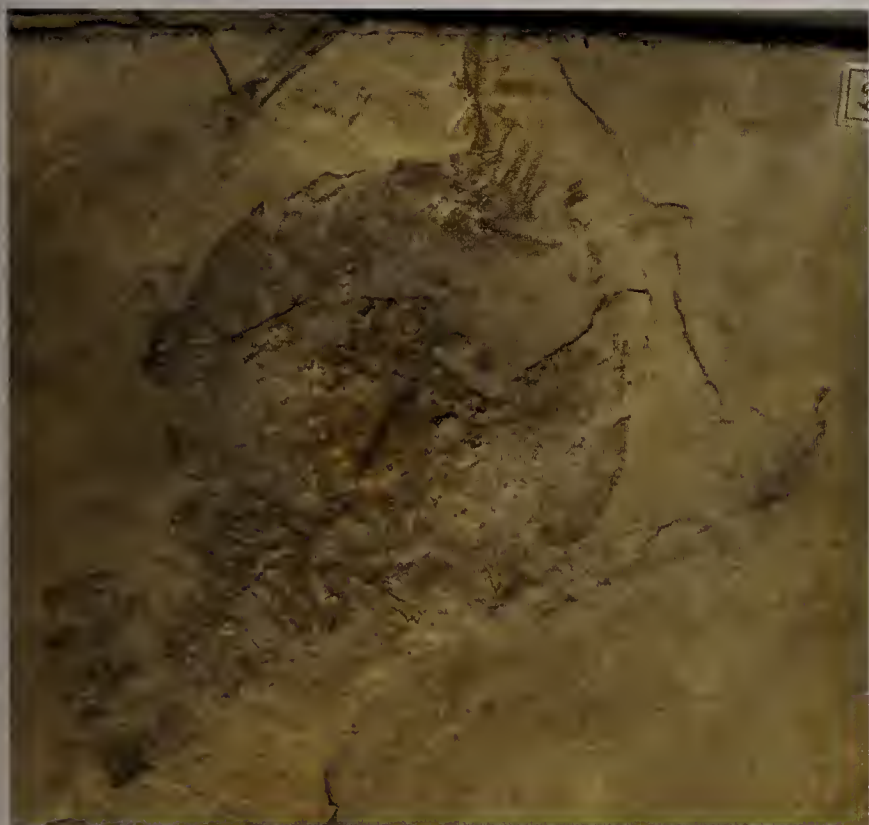
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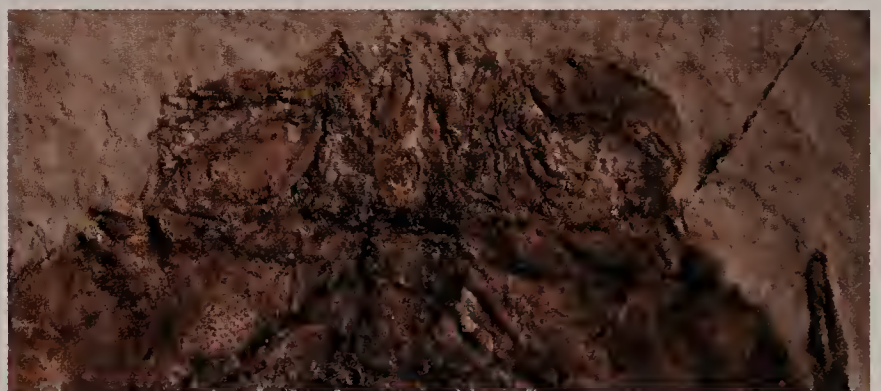
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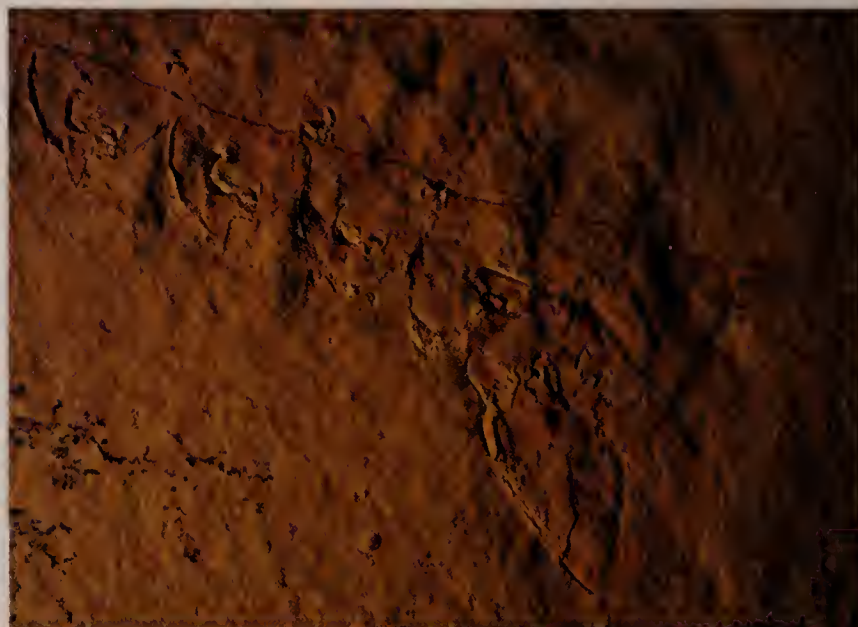
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MORPHOLOGY, TAXONOMY AND DIVERSITY OF VAMPYROPOD COLEOIDS (CEPHALOPODA) FROM THE UPPER CRETACEOUS OF LEBANON

MILANO MAGGIO 2006

Elenco delle Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano

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Morphology, taxonomy and diversity of vampyropod Coleoids (Cephalopoda) from the Upper Cretaceous of Lebanon

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Morphology, taxonomy and diversity of vampyropod Coleoids (Cephalopoda) from the Upper Cretaceous of Lebanon

Abstract - Morphology, taxonomy and diversity of coleoids from the Cenomanian and Santonian of Lebanon are described. Until hitherto, the coleoid fauna of the Late Cretaceous Lithograhic Limestones of Hâqel, Hjoûla (both Upper Cenomanian) and Sâhel Aalma (Upper Santonian) includes five vampyropod and only one belemnoid species. Decabrachia are unknown from these localities.

The comparatively poor information about the genus *Dorateuthis* Woodward, 1883 is discussed morphologically as well as taxonomically. *Rachiteuthis donovani,* a taxon newly introduced herein, is described for the first time. Specimens determined as *Trachyteuthis* cf. *hastiformis* Rüppel, 1829 extend the stratigraphical range of this genus from the Callovian up to the Cenomanian. Close morphological affinities of *Libanoteuthis libanotica* Fraas, 1878 with *Glyphiteuthis ornata* Reuss, 1854 from the Turonian of Bohemia (Czech Republic) suggest that *Libanoteuthis* Kretzoi, 1942 is a junior subjective synonym of *Glyphiteuthis* Reuss, 1854. Morphological knowledge about each taxon is improved by an exceptional high number of specimens, which are deposited in the Museo Civico di Storia Naturale di Milano (MSNM).

Key-words: Coleoidea, Vampyropoda, Cenomanian, Santonian, Lebanon.

Riassunto - Morfologia, tassonomia e diversità dei coleoidei vampiropodi (Cephalopoda) del Cretaceo superiore del Libano.

Vengono descritte la morfologia, la tassonomia e la diversità dei coleoidei del Cenomaniano e del Santoniano del Libano. Ad oggi, la fauna a coleoidei dei calcari litografici del Cretaceo superiore di Hâqel, di Hijoula (entrambi Cenomaniano superiore) e di Sâhel Aalma (Santoniano superiore) comprende cinque specie di vampiropodi e una sola specie di belemnoidi. In queste località non sono stati rinvenuti esemplari di Decabrachia.

Vengono discusse dal punto di vista morfologico e tassonomico le informazioni relativamente scarse sul genere *Dorateuthis* Woodward, 1883. Viene descritto per la prima volta *Rachiteuthis donovani*, un taxon precedentemente istituito e qui ripresentato. Gli esemplari ascritti a *Trachyteuthis* cf. *hastiformis* Rüppel, 1829 estendono la distribuzione stratigrafica di questo genere dal Calloviano fino al Cenomaniano. Le strette affinità morfologiche fra *Libanoteuthis libanotica* Fraas, 1878 e *Glyphiteuthis ornata* Reuss, 1854 del Turoniano della Boemia (Repubblica Ceca) inducono a considerare *Libanoteuthis* Kretzoi, 1942 come sinonimo juniore soggettivo di *Glyphiteuthis* Reuss, 1854. La conoscenza della morfologia di ogni taxon è accresciuta grazie al numero eccezionalmente alto degli esemplari a disposizione, depositati presso il Museo Civico di Storia Naturale di Milano (MSNM).

Parole chiave: Coleoidea, Vampyropoda, Cenomaniano, Santoniano, Libano.

INTRODUCTION

The Lithographic Limestones ("fish beds", "fish shales") of Lebanon (Hâqel, Hjoûla and Sâhel Aalma) are well-known for their well-preserved fossil assemblage. Especially fishes and crustaceans have been the subject of many publications (Garassino, 1994; Schram *et al.,* 1999; Forey *et al.,* 2003; Taverne & Filleul, 2003). By contrast, knowledge about Cephalopod coleoids is comparatively poor, although many beautiful specimens occur.

Coleoidea are typified by the extant squids, cuttlefishes and octopuses. According to Boletzky (2003) recent Coleoidea are classified into the eight-armed Vampyropoda and the ten-armed Decabrachia. The third coleoid superorder constitutes the extinct Belemnoidea (Late Carboniferous – Late Cretaceous). Within the Vampyropoda the Cirroctopoda and the Octopoda are grouped together as Octobrachia. The Octobrachia represent the sister taxon of the Vampyromorpha.

Decabrachia include the Sepiida, Spirulida, Idiosepiida, Sepiolida and the Teuthida. Although these groups are comparatively well known, their phylogenetic relationships are surprisingly problematic (Young & Vecchione, 1996; Vecchione *et al.,* 2000; Boletzky, 2003).

The fossil record of coleoid groups is usually biased towards the preservation of mineralised "hard parts". Discoveries of soft tissues are exclusively connected to so-called "Konservat-Lagerstätten". Their extraordinary preservational potential is the most important factor by which the poor morphological knowledge, and consequently the problematic phylogeny of the Coleoidea can be improved (Donovan, 1977; Engeser, 1990; Doyle *et al.,* 1994; Young *et al.,* 1998; Boletzky, 1999; Haas, 2002 and 2003). Well-known Lagerstätten with a comparatively high soft-part resolution are, for example, the Sinemurian of Osteno (Italy), the Toarcian of Holzmaden (Germany) and Yorkshire (England), the Callovian of La Voulte-sur-Rhône (France) and Christian Malford (England), the Tithonian of Solnhofen (Germany), the Cenomanian of Hâqel (Lebanon) and the Santonian of Sâhel Aalma (Lebanon). For palaeobiologists, these biotas form unique taphonomic and evolutionary windows through the Mesozoic, allowing detailed reconstructions.

The Late Cretaceous Lithographic Limestones of Lebanon display a soft-part preservation that rivals the famous German "Posidonienschiefer" of Holzmaden and the "Solnhofener Plattenkalke". So far five coleoid species (*Dorateuthis syriaca, Dorateuthis sahilalmae, Libanoteuthis libanotica, Palaeoctopus newboldi, Acanthoteuthis syriaca*) are known from these Late Cretaceous deposits. Several specimens of them (including Holotypes) are deposited in the museums of Berlin, Stuttgart (both Germany), Paris (France) and London (United Kingdom). However, the Museo Civico di Storia Naturale di Milano (Italy) as well as the Black Hills Institute of Geological Research in Black Hills (United States) house by far the largest collection of Lebanese coleoids. Neither the Milan nor the Black Hills specimens have ever been described. For the first time a large number of specimens allows a detailed morphological documentation and comparison. The description of both collections starts with the Milan specimens. A forthcoming project with Neal L. Larson (Black Hills Institute of Geological Research) describing the specimens of the Black Hills collection will comprise the entire cephalopod fauna of Hâqel.

PREVIOUS STUDIES ON COLEOID CEPHALOPODS FROM THE LATE CRETACEOUS OF LEBANON

First investigations of Lebanese coleoids began in 1846 with incomplete descriptions by Sowerby, who first mentioned *Calaïs Newboldi,* better known as *Palaeoctopus newboldi* Woodward, 1883, the first undoubted member of the Octopoda. More serious and detailed studies by Lartret (1877), Fraas (1878), and Woodward (1883, 1896) yielded two other members of the Coleoidea which are now assigned to the Vampyropoda: *Dorateuthis syriaca* Woodward, 1883 and *Libanoteuthis libanotica* Fraas, 1878.

In 1922 Naef established two additional taxa. One was erected by means of a doubtful specimen of Fraas, which Naef called "*Sepialites Sahil Almae*". This specimen (deposited in Stuttgart) is now considered to be the Holotype of *Dorateuthis sahilalmae.* Naef's other specimen, "*Beloteuthis libanotica*", was proved to be the isolated gladius element of *Palaeoctopus newboldi* (Haas, 2002; Bizikov, 2004).

Roger (1946) treated taxa such as *Palaeoctopus newboldi, Dorateuthis syriaca* and *Libanoteuthis libanotica* and established soft parts and hooks of the first Lebanese belemnoid *Belemnoteuthis (Acanthoteuthis) syriaca*, whose classification is admittedly uncertain.

Additional information on Lebanese coleoids comes from Engeser & Reitner (1986). They re-described the collection of Fraas as well as other Lebanese specimens accumulated in the Museum für Naturkunde Stuttgart (SMNS). They erected a new genus (*Parateudopsis*) and mentioned an uncertain species (*Palaeololigo* sp.). Both taxa have proved to belong to remains of *Palaeoctopus*.

GEOLOGICAL SETTING

Studied specimens are derived from the Cenomanian outcrops at Hâqel (45 km north of Beirut) and Hjoûla (10 km east of Byblos) as well as the Santonian outcrops of Sâhel Aalma (25 km north of Beirut) (Fig. 1). Today each site is exclusively quarried for fossils. In recent decades several authors have investigated these geological settings (Ejel & Dubertret, 1966; Hückel, 1970, 1974 and 1974b; Hemleben, 1977; Dalla Vecchia *et al.,* 2002).
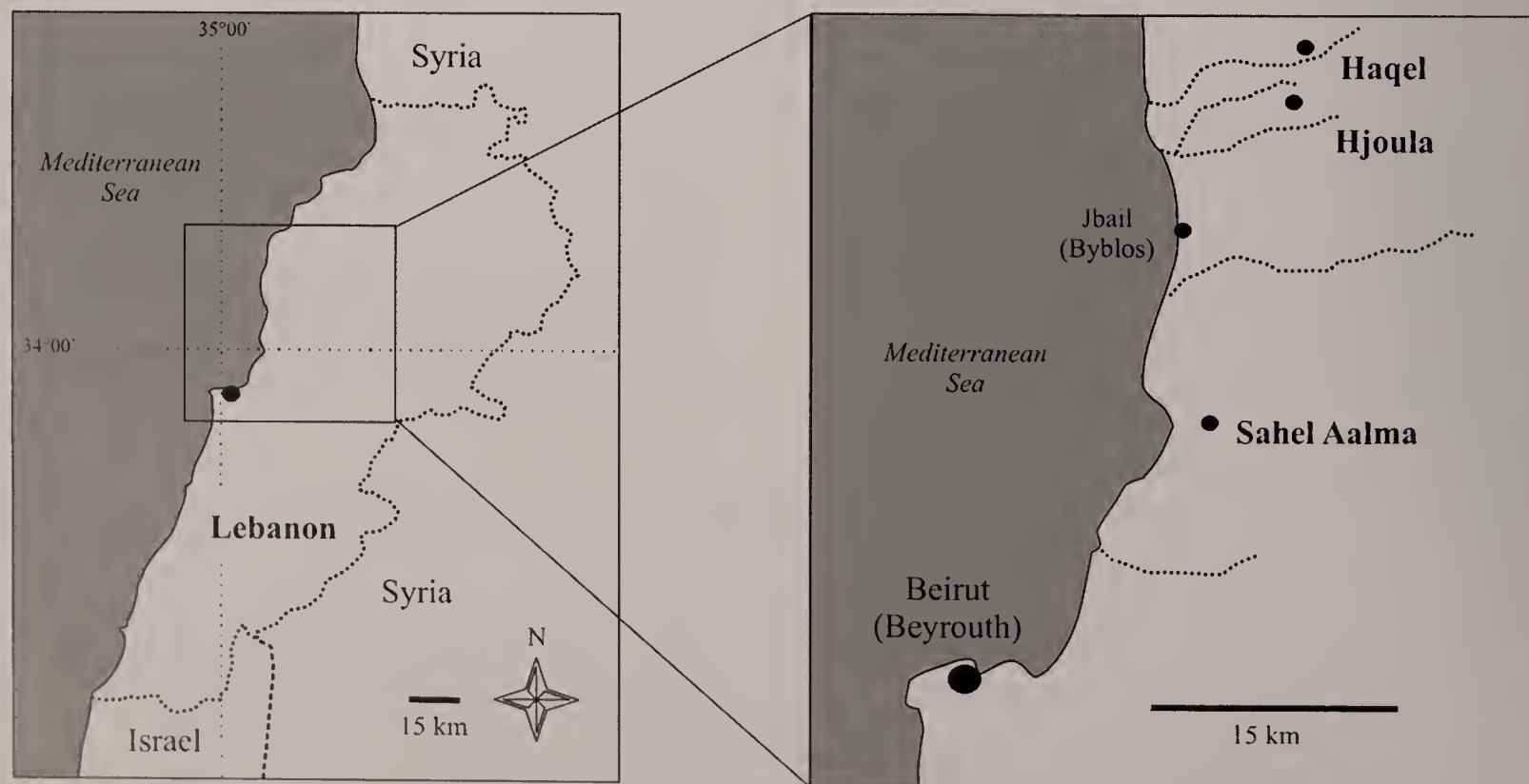
Fig. 1 - Locality map of Hâqel, Hjoûla and Sâhel Aalma.

The precise age of Hâqel and Hjoûla varies according to different authors. In his comprehensive sedimentological study Hückel (1970) divided the Cenomanian Limestones into seven units and concluded that Hâqel (unite V) and Hjoûla (unite IV) were deposited during the later Lower Cenomanian. Owing to the occurrence of the ammonite *Allocrioceras annulatum* as a member of the *Metoicoceras geslinianum* Zone, Wippich & Lehmann (2004) confirmed the conclusions of Hemleben (1977) and dated Hâqel and Hjoûla as Upper Cenomanian (Fig. 2). Dalla Vecchia *et al.* (2002) considered Hâqel and Hjoûla as lower Upper Cenomanian, because Nammoûra (another fossil-rich locality a few kilometres in the South of Hjoûla and slightly younger than Hâqel and Hjoûla) is dated as Middle Cenomanian

Sâhel Aalma, a locality with very similar depositional conditions and almost the same coleoid diversity, is commonly dated as Upper Santonian (Ejel-Dubertret, 1966; Garassino, 1994).

Each outcrop is of particular morphological importance, because fossils show precise preservation of soft tissues. The fauna consists of fishes (Forey *et al.*, 2003; Taverne & Filleul, 2003), crustaceans (Garassino, 1994; Schram *et al.*, 1999), echinoderms (Hückel, 1970), other molluscs (Forey *et al.*, 2003; Wippich & Lehmann, 2004) and worms (Dalla Vecchia & Venturini, 1999; Bracchi & Alessandrello, 2005), pterosaurs (Dalla Vecchia *et al.*, 2001) and other reptiles (Dal Sasso & Pinna, 1997; Dalla Vecchia & Venturini 1999; Rieppel & Head, 2004; Caldwell, 2006 in press; Tong *et al.*, 2006).

Palaeogeographers believe that the sediments of Hâqel and Hjoûla were deposited at the edge of the Thethian shelf margin, 400 km away from the ancient coastline (Hembleben, 1977; Philip *et al.*, 1993). The map in Fig. 3 illustrates the palaeogeographic situation of the Central Tethys during the Cenomanian. Hückel (1970) found that Hâqel and Hjoûla were deposited in small basins. Most authors agree that the "fish beds" were formed in an anoxic environment. Hemleben (1977) suggested that upwelling at the shelf margin occasionally supported blooms of protists or "red tides", which caused episodes of mass mortality. Deoxygenated bottom water and high sedimentation rates then prevented the decay of dead bodies.
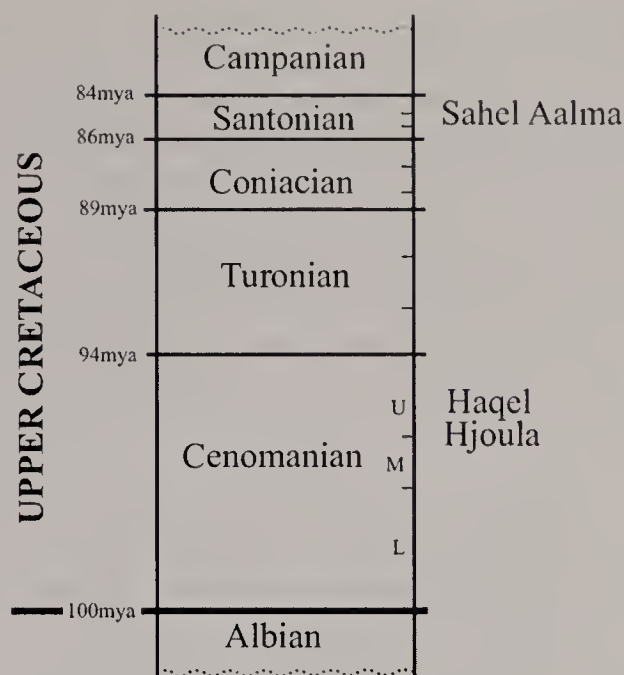
Fig. 2 - Stratigraphic age of Hâqel, Hjoûla and Sâhel Aalma.

Fig. 3 - Palaeogeographic map of the Central Tethys during the Late Cenomanian. L = Lebanon. Modified after Philip *et al.* (1993).

MATERIAL

The study was conducted on 38 specimens belonging to the Museo Civico di Storia Naturale di Milano (MSNM). Most specimens come from Hâqel and Hjoûla. Only two specimens come from Sâhel Aalma. Material from Nammoûra was not available.

Specimens were investigated in detail with a binocular microscope. Oblique light reveals faint structures, which were not recognized under vertical light conditions. Ultraviolet light was used to indicate phosphatised soft tissues. A number of additional specimens from different localities (including Holotypes housed in collections of Berlin, Stuttgart, London, Paris Vienna, and Prague) were used as comparative material.

MODES OF PRESERVATION

All specimens are compressed and flattened on a 2-dimensional surface. Although the mineralogy was not analysed, gladii (singular "gladius": a stiff supporting structure in the dorsal mantle, see below) were most probably preserved as francolite. However, francolite is a diagenetical result. On the assumption that vampyropod gladii derived from a belemnoid organic proostracum, a purely organic composition is reasonable (Hewitt & Wignall, 1988; Doguzhaeva & Mutvei, 2003; Fuchs *et al.*, submitted).

Konservat-Lagerstätten are characterised by a detailed preservation of soft tissues. According to Allison (1988), Allison & Briggs (1991), Wilby (1993), Kear *et al.* (1995) and Wilby & Briggs (1997), the highest-fidelity preservation occurs where muscular structures are post-mortem mineralised in apatite (a calciumphosphate).

Soft-part preservation of coleoids is various. Only in rare cases the specimens include articulated bodies complete with mantle, arms, retractors and fins. Typically, coleoids are only partially mineralised and disarticulated, but mineralisation of the mantle in close association with arm stubs occurs often. Jaw preservation is common, and occasionally stomach contents as well.

An ink sac occurs in almost each specimen, but the possession of ink is not considered to be a diagnostic feature within coleoids and is therefore neglected in the descriptions.

SYSTEMATIC PALAEONTOLOGY

Subclass Coleoidea Bather, 1888
Superorder Vampyropoda Boletzky, 1992
Suborder Prototeuthina Naef, 1921
Family Plesioteuthididae Naef, 1921
Genus *Dorateuthis* Woodward, 1883

Type species: *Dorateuthis Syriaca* Woodward, 1883; by monotypy.

Stratigraphical range: Upper Cenomanian of Hjoûla and Upper Santonian of Sâhel, Lebanon.

Remarks: Woodward (1883) first described *Dorateuthis syriaca* from Sâhel Aalma. Later-treated specimens of *Dorateuthis syriaca* as well as specimens assigned to *Dorateuthis sahilalmae* derived from Sâhel Aalma. However, as it will be shown, *Dorateuthis* already occurred in the older Cenomanian of Hjoûla.

The placement of the genus *Dorateuthis* within the Leptotheuthididae, Naef 1922 by Jeletzky (1966: 45) and other authors cannot be accepted. The view of Jeletzky (1966) is based on a doubtful reconstruction given by Roger (1946: 14, Figs. 6-7). After re-study of Roger's specimens in Paris there are no doubts that the genus *Dorateuthis* has more in common with *Plesioteuthis* or *Senefelderiteuthis* than with *Leptotheuthis*. Thus we follow the classification of Donovan (1977) and Engeser & Reitner (1986) in placing the genus *Dorateuthis* within the Plesioteuthididae.

Dorateuthis cf. *syriaca* Woodward, 1883 (Pls. I-III)

1883 *Dorateuthis Syriaca* n. sp. – Woodward, p. 1 ff., Pl. 1.
1888 *Curculionites senonicus* – Kolbe, pp. 135-136, Pl. 11, Fig. 8.
1920 *Dorateuthis Syriaca* Woodward – Bülow-Trummer, p. 262.
1922 *Sepialites Sahil-Almae* – Naef, p. 134, Fig. 49.
1922 *Dorateuthis syriaca* Woodward, 1883 – Naef, p. 135, Fig. 50.
(?)1932 *Doratoteuthis syriaca* H. Woodward – Quenstedt, p. 186 ff.
1946 *Leptoteuthis syriaca* Woodward – Roger, p. 14 ff., Fig. 6-7, Pl. 4, Fig. 5-6, Pl. 9, Fig. 1.
1966 *Dorateuthis syriaca* – Jeletzky, pp. 44-45.
1977 *Plesioteuthis syriaca* – Donovan, p. 40.
1982 *Dorateuthis syriaca* Woodward – Reitner & Engeser, p. 215.
1986 *Dorateuthis syriaca* Woodward, 1883 – Engeser & Reitner, p. 4.
1986 *Dorateuthis sahilalmae* (Naef, 1922) – Engeser & Reitner, p. 4, Fig 1, Pl. 1, Fig. 1.
1986 *Dorateuthis* sp. – Engeser & Reitner, p. 5, Pl. 1, Fig. 2.
1987 *Dorateuthis syriaca* Woodward, 1883 – Riegraf, p. 97.
1988 *Dorateuthis syriaca* Woodward, 1883 – Engeser, p. 42.
2002 *Maioteuthis* n. sp. – Novati 2002, p. 88.
2004 *Dorateuthis syriaca* Woodward – Lukeneder & Harzhauser, p. 3.

Holotype: specimen of Woodward (1883, Pl. 1), BMNH C 5017 (Pl. III, Fig. B).

Locus typicus: Sâhel Aalma, Lebanon.

Stratum typicum: Lithographic Limestones of Sâhel Aalma, Upper Santonian.

Geographic and stratigraphic distribution: Upper Cenomanian of Hjoûla – Upper Santonian of Sâhel Aalma, Lebanon.

Material: eight specimens were investigated: MSNM i25144 (Pl. I, Figs. A-B), i24800 (Pl. II, Fig. A), i25133 (Pl. II, Fig. B), i25134 (Pl. III, Fig. A), i25128, i24802 originated from Hjoûla, whereas i23108 (Pl. I, Fig. C) and i26092 come from Sâhel Aalma.

Description

Gladius: specimens MSNM i25144 (Pl. I, Fig. A), i23108 (Pl. I, Fig. C), i25128 and i26092 are seen either in dorsal or ventral views whereas specimens i24800 (Pl. II, Fig. A), i25133 (Pl. II, Fig. B), i25134 (Pl. III, Fig. A) and i24802 are embedded laterally. Lateral specimens provide less information about gladius characteristics. In comparison to dorsoventral specimens, lateral examples provide more information about soft-body morphology than gladius characteristics. The reconstruction in Fig. 4 is only tentative, because each gladius of *Dorateuthis* is in a bad condition.

Only in specimen MSNM i25144 are imprints of a complete gladius preserved (Pl. I, Fig. A). It is embedded dorsoventrally and seen in dorsal view. The total length of the gladius is 7.5 cm. Its anterior end is 0.8 cm in width. Compared to the length of other specimens MSNM i25144 is a juvenile (MSNM i25134 is longest with at least 24 cm). More information about the maximum width of other specimens is not worthwhile owing to incomplete preservation, compaction or lateral embedment.

In MSNM i25144 (Pl. I, Fig. A) and i23108 (Pl. I, Fig. C) pronounced lateral ridges are rounded and ca. 1 mm in width. Their increase in thickness throughout the whole length is insignificant. Both ridges diverge at an angle of approximately 7°. Lateral ridges must be regarded as lateral swellings of the median field.
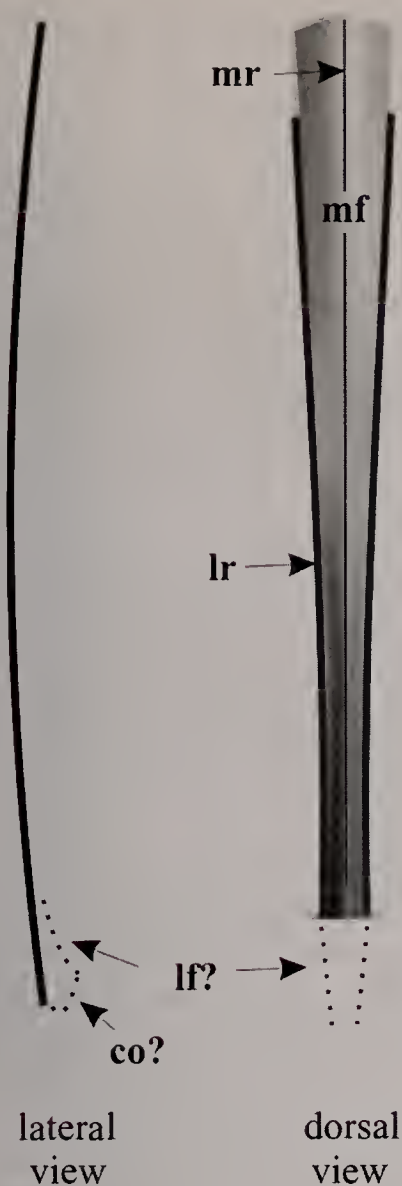
Fig. 4 - *Dorateuthis syriaca.* Reconstruction of the gladius. The morphology of the posterior gladius end is uncertain. co = conus; lf = lateral field; lr = lateral ridge; mf = median field; mr = median ridge.

A distinct median line or ridge can be observed in specimen MSNM i23108 (Pl. I, Fig. C) and i26092. In the latter the line is seen to reach the most anterior end of the gladius.

The anteriormost extremity of the gladius and growth lines on the gladius surface are poorly preserved, but there are no indications for a pointed anterior end.

Imprints on both sides of this posterior end observable in specimen MSNM i25144 (Pl. I, Fig. B) are probably imprints of lateral fields (conus fields). If they are indeed lateral fields they are extremely narrow and short (2 mm in width and 2.1 cm in length respectively). However, lateral specimens do not confirm this assumption.

Lateral specimens MSNM i24800 (Pl. II, Fig. A) and i25133 (Pl. II, Fig. B) demonstrate the original curvature of the gladius, which probably reflects its tension within the mantle sac.

Arms: specimens MSNM i25133, i25134 and i26092 exhibit arm preservation. The first two show at least three arms (Pl. II, Fig. B; Pl. III, Fig. A), the latter at least four. In this specimen arms preserved as phosphatised musculature are only fragmentary and apparently tangled. It seems worthwhile to note that the diameters of the arms are relatively thick. In MSNM i26092 one arm is at least 5 cm long. Ultraviolet light supplies no further information, so that reliable measuring data are not available. Neither tentacles, clubs, suckers nor cirri are discernible anywhere.

Head: in four specimens the position of the head can be presumed (MSNM i25133, i25134, i24800, i26092) from the buccal mass. Strongly phosphatised structures between the arms and the mantle interpreted as the buccal mass are displaced from the mantle edge. In MSNM i24800 (Pl. II, Fig. A), i25133 (Pl. II, Fig. B) and i25134 (Pl. III, Fig. A) the buccal mass is located some distance in front of the anterior gladius end. Ultraviolet light suggests that the anterior end of the gladius reaches the anterior mantle margin. This indicates that the head was apparently demarcated. Beaks were not observed.

Fins: in specimens MSNM i25128 and i25134 imprints of fins are present. In lateral specimen MSNM i25134 (Pl. III, Fig. A) preparation has laid open a ca. 3 cm long weak lobate structure, which is considered to be a fin. Similar lobate structures are also present in MSNM i25128. However, in both cases this is not beyond doubt, as ultraviolet light did not confirm this assumption.

Stomach: in specimen MSNM i25144 stomach contents are preserved (Pl. I, Fig. A). As in recent coleoids the stomach is situated between the ink sac and the rear of the mantle cavity. Ingested food largely consists of fish remains, so *Dorateuthis* was certainly an active predator. As correctly suggested by Lukeneder & Harzhauser (2005) the mass of food indicates the presence of a crop (caecum).

Remarks: the Milan specimens of *Dorateuthis syriaca* are the first evidence of this taxon in the Cenomanian. However, morphological knowledge about the genus *Dorateuthis* (including both species) is still comparatively scarce. This is partly due to a very flimsy gladius. After re-investigation of the Holotypes of *Dorateuthis syriaca* (Pl. III, Fig. B) and *Dorateuthis sahilalmae* (Pl. III, Fig. C) and other examples of this genus in collections from Berlin, Stuttgart, Vienna, Paris and London and comparison with the Milan specimens described herein (including the Milan specimens a total amount of 27 specimens of this genus were investigated) it can be concluded that only the lateral ridges and partly the median ridge have the potential to withstand decay. Often we have just hollow imprints of the massive lateral ridges. Because of its narrowness the median field has apparently no preservational potential. However, long and wide lateral fields as suggested by Roger (1946) can be excluded. If lateral fields were present in this genus, they must have been extremely short and narrow as reconstructed in Fig. 4.

Further, it cannot be ruled out that the gladius is sometimes disrupted longitudinally. In the author's opinion, differing information about apical angles ranging from 7° to 25° is a result of disruption and distortions. In spite of this observation, the two representatives of the genus are differentiated by means of their apical angles. According to Engeser & Reitner (1986: 4) *D. sahilalmae* (Pl. III, Fig. C) is mainly distinguished from *D. syriaca* by a larger apical angle and a bigger ink sac. The latter is here considered to be highly dependent on the volume of ink within the sac just before death and on random preservational compaction. None of the 27 specimens of *Dorateuthis* investigated showed a correlation between ink sac size and the apical angle. Thus an unambiguous character distinguishing *D. sahilalmae* from *D. syriaca* is still missing.

Re-investigation of the arms of the Holotypes of *D. syriaca* Woodward, 1883 as well as *D. sahilalmae* Naef, 1922 has shown that this genus is certainly an eight-armed coleoid. A specimen from the Naturhistorisches Museum Wien exhibits the best-preserved arm crown consisting of eight distinct arms (Pl. II, Fig. C, original of Lukeneder & Harzhauser, 2004). There are absolutely no indications for the presence of tentacles as proposed by Woodward (1883). However, in cases where arm musculature is preserved it appears that some animals had well-developed, fleshy arms (c.f. MSNM i26092), while others seem to have had comparably thin arms (Pl. II, Fig. C; Pl. III, Fig. B). A tentative ontogenetical correlation for thickest and longest arms is observed in specimens with a gladius longer than 20 cm. On the other hand, thinner and shorter arms are associated with gladii shorter than 10 cm. Therefore different ontogenetical stages might explain variable arm morphology. Alternatively, inconsistencies are more likely due to incorrect preparation or incomplete preservation than to a specific or an ontogenetic character. Unsuccessful correlation between arm thickness and gladius characteristics confirms these considerations. As a result, presence of two species within the genus *Dorateuthis* remains doubtful.

Likewise, no distinct differences were found between specimens from Hjoûla, and Sâhel Aalma. Thus, gladius, ink sac and arm morphology are still useless as distinguishing characters. From Hâqel *Dorateuthis* is still unknown. Perhaps, the undescribed material housed in the Black Hills Institute may provide additional information. Until then, confirmation of two separated species from Sâhel Aalma as well as erection of a new species from Hjoûla would be premature.

Suborder Teudopsidina Starobogatov, 1983
Family Palaeololiginidae Naef, 1921
Genus *Rachiteuthis* (n. gen.)

Derivatio nominis: from rachis-like appearance of the gladius.

Type species: *Rachiteuthis donovani* (n. sp., by monotypy).

Locus typicus: Hjoûla (Lebanon).

Stratum typicum: Lithographic Limestones of Hjoûla, Upper Cenomanian.

Geographic and stratigraphic distribution: known only from the locus typicus and stratum typicum.

Diagnosis: palaeololiginid with a spear- or shaft-like gladius; lateral fields spread out and short with a weak hyperbolar zone; conus reduced; free rachis elongated; distinct lateral ridges and a median unornamented keel extend from posterior to anterior extremities; body torpedo-shaped; insertions of triangular fins comparatively broad; arms comparatively slender.

Remarks: the genus is placed within the Palaeololiginidae because of common possession of a sharply pointed free rachis. Presence of lateral ridges similar to members of the Plesioteuthididae may also imply an affiliation to these forms. However, in contrast to the ventrally closed true conus of *Plesioteuthis*, the new genus shows a reduced (opened) conus with outspread lateral fields.

Rachiteuthis donovani (n. sp.) (Pls. IV-VI)

1977 "*Plesioteuthis*-like gladii" – Donovan, p. 40.

Derivatio nominis: the name is in honour of D. T. Donovan and his exceptional merits in palaeontological malacology.

Holotype: MSNM i25142 (Pl. IV).

Paratype I: MSNM i25135 (Pl. V, Fig. A).

Paratype II: MSNM i25139 (Pl. V, Fig. B).

Locus typicus: Hjoûla (Lebanon).

Stratum typicum: Lithographic Limestones of Hjoûla, Upper Cenomanian.

Geographic and stratigraphic distribution: known only from the locus typicus and stratum typicum.

Remarks: in 2002 Novati already recognized and suggested this new taxon, but never described it. The taxon name was therefore a nomen nudum. Present author decided to keep the taxon name and to present the first description of *Rachiteuthis*.

Material: five specimens were investigated: MSNM i25142, i25139, i25135, i25132a+b and i25143. The latter specimen is a juvenile and provides little additional information, but the former are adult and each of them bears interesting features. Specimen MSNM i25142 is selected as the Holotype because a complete gladius with detailed structural morphology is preserved. Although the gladius of Paratype I (MSNM i25135) is only preserved as imprints, this specimen exhibits extraordinary soft-part preservation, including arms, head, funnel, ink sac and fins. Paratype II shows the lateral view of this taxon.

Description

Gladius: the Holotype (Pl. IV) exhibits by far the best-preserved gladius. Because it is completely dorsoventrally embedded, the obtained measurements are highly usable (data from gladii of the Paratypes are ambiguous for they are more or less laterally compressed and are thus not considered here). Additionally, gladius characteristics of the Holotype are preserved 3-dimensionally (Fig. 5).

Imprints of the ventral surface are visible where gladius material is missing. The Holotypes gladius dimensions (Fig. 5) are as following:

- gladius length (gl): 5.7 cm
- lateral field length (lfl): 1.3 cm
- median field width (mfw_{lf}) at the end of the lateral fields: 0.35 cm
- maximum median field width (mfw_{max}): 0.59 cm
- maximum lateral field width (lfw): 0.82 cm
- lateral field length/gladius length (lfl/gl): 0.23
- median field width/gladius length (mfw_{max}/gl): 0.1
- median field width/gladius length (mfw_{lf}/gl): 0.06
- lateral field width/lateral field length (lfw/lfl): 0.6
- apical angle (angle of diverging inner asymptotes): 8°

Lateral field length (lfl) accounts for 23% of total gladius length (gl). In other investigated specimens it varies between 23 and 26%, but as already mentioned, this is presumably due to different degree of compaction. An undetermined specimen from Hjoûla in the Museum of Natural History in London (Donovan, 1977: 40, "*plesioteuthis*-like
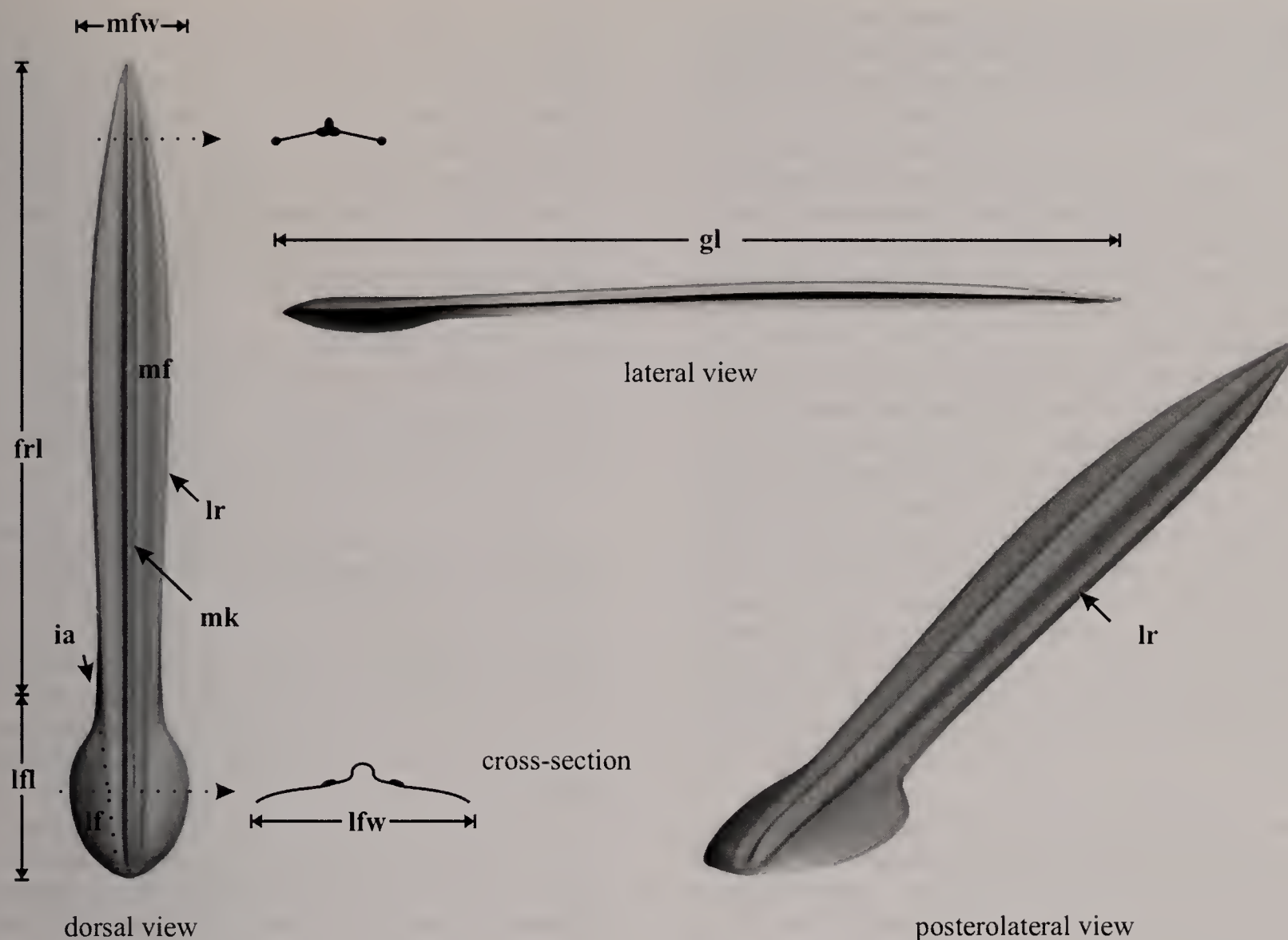
Fig. 5 - *Rachiteuthis donovani*. Reconstruction of the gladius. frl = free rachis length; gl = gladius length; ia = inner asymptote; lf = lateral field; lfl = lateral field length; lfw = lateral field width; lr = lateral ridge; mf = median field; mfw = median field width; mk = median keel.

gladii"; register number BMNH C 28408) is identical with the present taxon and shows the same lfl/gl - ratio of 0.23.

The maximum width of the median field (mfw_{max}) is 0.59 cm, measured half way along the rachis-like median field (free rachis). This yields an mfw_{max}/gl - ratio of 0.1. The anterior extremity of the gladius is sharply pointed. From posterior to anterior a constantly 0.7 mm thick rounded massive keel is prominent on the median field. Imprints of the ventral gladius surface in the anterior part (where gladius material is missing) show that the median keel is ventrally two-parted (see cross-section Fig. 5; Pl. IV, Fig. B). Since these structures are not present on the dorsal surface, the ventral surface differs from the dorsal surface. On both sides of the keel lateral ridges form outermost margins. These are also counter drawn on the ventral surface, as shown by imprints where gladius material is not preserved (Pl. IV, Fig. B).

The lateral fields appear very thin, marginally even translucent. Growth lines on the dorsal surface of both lateral fields can be easily traced but exhibit just a weakly curved hyperbolar zone (Pl. IV, Fig. C). This implies that outer asymptotes are present but inconspicuous. Inner asymptotes divide the lateral and the median field and are thus well marked by lateral ridges. Lateral ridges diverge at an angle of 8°.

Arms: as already mentioned, especially Paratype I (Fig. 6; Pl. V, Fig. A; Pl. VI, Fig. B) displays an arm crown contrasting with the surrounding colour of sediment (surprisingly they are not preserved as phosphatised musculature). At least six arms can be counted. A seventh arm is only visible under ultraviolet light (Pl. VI, Fig. B). They are all uniform and slender (approximately 5 cm in length and 0.3 mm in diameter).

In Paratype II (Pl. V, Fig. B; Pl. VI, Fig. C), arms are preserved as 3-dimensional ridges similar to those described from *Münsterella scutellaris* (Fuchs *et al.*, 2003: 4). As in lateral specimens of *M. scutellaris*, ultraviolet light reveals the phosphatised musculature of four arms, which are considered to be the right arms of each pair. There is no indication of an arm web between the
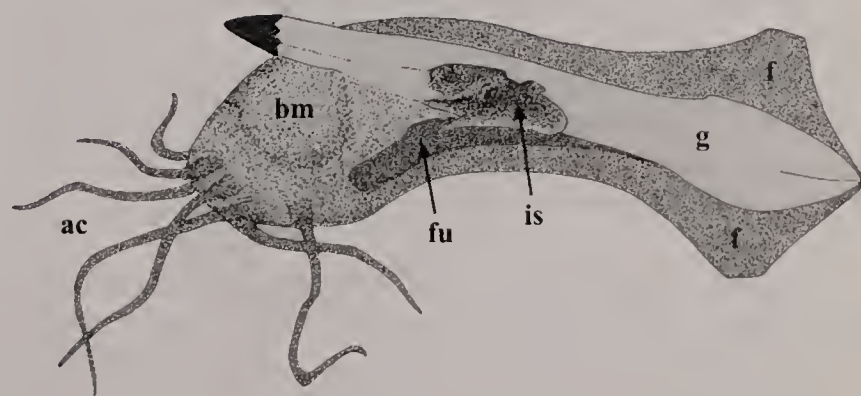
Fig. 6 - *Rachiteuthis donovani*. Drawing of Paratype I (MSNM i25135). ac = arm crown; bm = buccal mass; f = fin; fu = funnel; g = gladius; is = inc sac.

ridges. At least the inner surface of one left arm is preserved (most probably the ventrolateral arm). Tentacles, tentacle clubs, suckers or cirri are not observable in any of the specimens.

Head: neither in the Holotype nor in the Paratypes is there any reason to suppose a clearly demarcated head. In both Paratypes it seems that dorsal arm bases are a direct continuation of the dorsal mantle edge (Pls. V and VI). A head-mantle fusion would imply that the head was not clearly demarcated.

From specimens of *Münsterella scutellaris* (Fuchs *et al.*, 2003: 4) it was demonstrated that head retraction was possible in this taxon. Similar abilities are assumed for *Rachiteuthis*. The arm bases of both Paratypes lie very close to the anterior end of the gladius, which should mark the anterior mantle edge. The buccal mass of Paratype I is obviously situated within the mantle (Pl. V, Fig. A). Subsequently the head must have been retracted. This is not the case in the Holotype, where the head is apparently a short distance in front of the anterior end of the gladius and thus presumably stretched out. A head retractor muscle, which is observed in *Münsterella,* is not preserved.

Beaks: a weak parabolic structure within the head region of the Holotype is determined as a lower or upper beak but contains no real morphological information as obtained from *Trachyteuthis, Plesioteuthis or Leptoteuthis* from Nusplingen (Klug *et al.,* 2005).

Body outline: exceptional preservation of Paratype I allows statements about the complete body outline of *Rachiteuthis* (Pl. V, Fig. A). The body was apparently twisted during diagenesis. Although the funnel and soft-body are laterally embedded, gladius and fins are seen in dorsal view. During decay, the stiff gladius must have penetrated the anterior mantle. However, it is assumed that the body was nearly circular in cross-section and comparatively longish and slender (torpedo-shaped).

Funnel: funnel preservation is extremely rare even in Konservat-Lagerstätten. In Paratype I (Fig. 6; Pl. V, Fig. A) a structure determined as the funnel is situated beneath the anterior part of the gladius. It is 0.6 cm in diameter. The length is difficult to define. It is obvious that ink was ejected through the funnel. Like the head, the funnel seems to be retracted.

Fins: although phosphatised musculature is missing in Paratype I, posteriorly a triangular outline of paired fins is clearly visible (Fig. 6; Pl. V, Fig. A). The outer corners are distinctly rounded. They begin with the posteriormost extremity of the gladius and end 4.5 cm anterior to this point. Their rounded margins are 4.8 cm apart.

Differential diagnosis: gladius characteristics such as opened conus with comparatively short lateral fields, presence of a hyperbolar zone on the lateral fields as well as a distinctly pointed anterior end justify the taxonomic position within the Teudopsidina.

The presence of a median keel and paired lateral ridges in connection with a shaft-like prolongation of the rachis-like median field resembles *Palaeololigo oblongata* Wagner, 1859 or *P. albersdoerferi* Engeser & Keupp, 1999 from the Lithographic Limestones of Solnhofen. In contrast, the free rachis of *Rachiteutis* is much longer and the hyperbolar zone is less distinct than in *Palaeololigo.* A median keel and lateral ridges also occur in forms like *Plesioteuthis* and *Dorateuthis*. Compared to these forms lateral fields of *Rachiteuthis* do not form a closed conus but are clearly spread out.

Family Trachyteuthididae Naef, 1921
Genus *Trachyteuthis* v. Meyer, 1846
(= *Coccoteuthis* Owen, 1855; *Voltzia* Schevill, 1950; junior subjective synonyms)

Type species: *Sepia hastiformis* Rüppell, 1829 (by subsequent designation (Bülow-Trummer, 1920: 248).

Geographic and stratigraphic distribution: previous records of the genus *Trachyteuthis* are from the Callovian of Christian Malford, England (Martill & Hudson, 1994), the Oxfordian of Chile (Schulze, 1989), Graham Land of Antarctica (Doyle, 1991) and Viñales region of Cuba (Schevill, 1950), the Upper Kimmeridge of Dorset, England (Donovan, 1977) and Nusplingen, Germany (Klug *et al.,* 2005), the Tithonian of Solnhofen and the Volga region in Russia (Hecker & Hecker, 1955), the Aptian of Northwest Queensland, Australia (Wade, 1993) and Heligoland, Germany (Engeser & Reitner, 1985).

As the following descriptions show, we are now able to extend the stratigraphical range of *Trachyteuthis* at least up to the Upper Cenomanian.

Remarks: many workers have considered this genus to be a decabrachian, because of granulation on the dorsal surface of the gladius similar to recent cuttlebones of *Sepia* (Donovan, 1977; Doyle, 1991). Despite hundreds of well-preserved specimens from Nusplingen and Solnhofen there are no indications for a chambered complex associated with the gladius. Additionaly, specimens with ten arms have never been observed. Finally, Donovan (2002) presented a specimen of *Trachyteuthis* with two pairs of fins. This character is only shared with the recent *Vampyroteuthis infernalis*. Except granulation, characteristic features for a decabrachian affiliation are absent. Therefore *Trachyteuthis* must ultimately be treated as a real representative of the Vampyropoda (Bandel & Leich, 1986; Doyle *et al.,* 1994; Donovan, 2002; Haas, 2002; Bizikov, 2004).

Trachyteuthis cf. *hastiformis* Rüppel, 1829 (Pl. VII)

Holotype: Senckenberg Museum, Frankfurt/Main (Germany), register number XI 1328.

Locus typicus: Lithographic Limestones of Solnhofen.

Stratum typicum: Lithographic Limestones of Solnhofen, Lower Tithonian (Malm, ζ 2b).

Geographic and stratigraphic distribution: as for the genus (?).

Material: MSNM i20591 (Pl. VII), MSNM i20590 and MSNM i25145 come from the locality of Hâqel.

Description

In each specimen parts of the gladius as well as mantle musculature are preserved. Neither ink sac, fin, head nor arm crown are observable in any of the specimens.

In MSNM i25145 mainly muscular mantle is preserved. The total length of this specimen is 26 cm. In most places musculature traces the outline of the anterior part of the gladius. Marginal remains of the gladius are still present at the anteriormost end, and one can follow the characteristically pointed anterior margin of the *Trachyteuthis* gladius. At a distance of 14 cm from this margin at a small spot in the median line, characteristic growth lines are "shining" through the musculature. Specimen MSNM i20590 is in such a poor condition that its identification as *Trachyteuthis* is merely presumed.

Specimen MSNM i20591 (Fig. 7; Pl. XII) displays a complete outline of the gladius. The gladius was embedded dorsally and is seen in ventral view. The majority of gladius material is originally preserved. Imprints of the dorsal surface are visible, where gladius material is missing. Measurements are as follows:
- gladius length (gl): 36.0 cm
- lateral field length (lfl): 14.5 cm
- median field width (mfw_{lf}) at the anterior end of the lateral fields: 9.0 cm
- maximum lateral field width (lfw_{max}): 13.0 cm
- lateral field length/gladius length (lfl/gl): 0.4
- maximum median field width/gladius length (mfw_{max}/gl): 0.25
- maximum lateral field width/lateral field length (lfw_{max}/lfl): 0.9

Owing to the ventral view there is nothing visible from the typical dorsal granulation. However, at the posteriormost end of the gladius weak imprints of granulations are visible similar to those of *Trachyteuthis hastiformis* from Solnhofen and Nusplingen.

Although the ends of the lateral fields are well preserved, a hyperbolar zone (as the transition from the lateral fields into the median field) is indistinct. As a result inner and outer asymptotes are merely conjecturable. Inner asymptotes diverge at an apical angle of approximately 37°. Inner asymptotes are commonly defined as the end of the lateral fields. Diverging structures on the median field should not be mistaken for inner asymptotes. The area between these structures is considered to be the granulated part of the median field. This granulated median part is stronger developed than marginal parts of the median field and diverges at an angle of approximately 10°. A well-preserved dorsal view of a *Trachyteuthis*-gladius from Nusplingen, illustrated in Klug *et al.* (2005), displays an identical dorsal strengthening.

Each ratio enumerated above as well as the apical angle fits well within the ranges known from specimens from Solnhofen and Nusplingen.

Differential diagnosis: present specimens are unambiguous representatives of the genus *Trachyteuthis* and are very close to *T. hastiformis* from Solnhofen and Nusplingen. Compared to a close relative from Hâqel and Sâhel Aalma, *Glyphiteuthis* (=*Libanoteuthis,* see below), *Trachyteuthis* cf. *hastiformis* differs in its much bigger dimensions and the lack of a median keel.
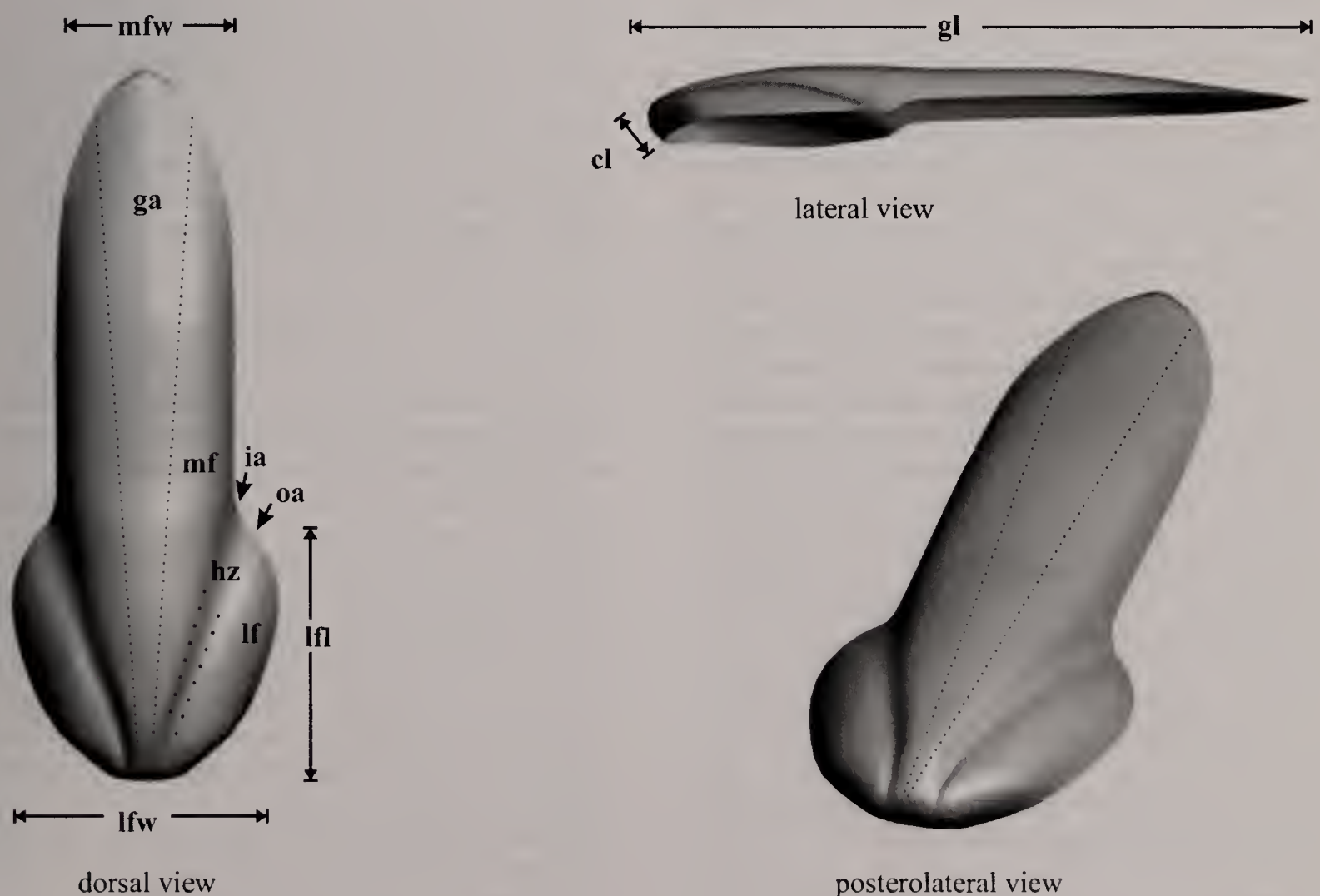
Fig. 7 - *Trachyteuthis* cf. *hastiformis*. Reconstruction of the gladius. cl = conus length; ga = granulated area; gl = gladius length; hz = hyperbolar zone; ia = inner asymptote; lf = lateral field; lfl = lateral field length; lfw = lateral field width; mf = median field; mfw = median field width; oa = outer asymptote.

Remarks: an unusual high number of specific names exist in the literature for forms of *Trachyteuthis hastiformis* from the Solnhofener Plattenkalks. Although Engeser (1988) regarded them altogether in synonymy, the presence of more than only one morphospecies cannot be ruled out (Fuchs, 2006). Further, species of the genus *Trachyteuthis* from other locations than Solnhofen cannot be clearly distinguished from *T. hastiformis* by means of adequate characters. Finally, there are no distinct differences in proportions even between Jurassic and Cretaceous examples. Since the first occurrence of the genus in the middle Jurassic no modifications are observable at first glance. As already mentioned by Donovan (1995) a comparative examination is necessary in order to specify morphological differences. Therefore, these specimens are provisionally determined as *Trachyteuthis* cf. *hastiformis*.

Genus *Glyphiteuthis* Reuss, 1854 (Pls. VIII-IX)

Type species: *Glyphiteuthis ornata* Reuss, 1854.
Geographic and stratigraphic distribution: Lower/Middle Turonian of Bílá Hora Formation (Czech Republic), Upper Cenomanian of Lebanon and Normandy (France), Upper Santonian of Sâhel Aalma (Lebanon).

Remarks: previously nobody has referred to the difficult morphological distinction between the Turonian genus *Glyphiteuthis* Reuss, 1854 from Bohemia (Czech Republic) and *Libanoteuthis* Kretzoi, 1942 from Hâqel, Hjoûla and Sâhel Aalma. Kretzoi (1942) erected *Libanoteuthis* without any descriptive explanations. While Roger (1946), Rioult (1962), Waage (1965), Engeser & Reitner (1986) and Engeser (1988) have used this genus name, Jeletzky (1966) and Donovan (1977) have placed this taxon within the genus *Trachyteuthis*. Certainly, there are enough morphological differences between the genera *Libanoteuthis* and *Trachyteuthis*. Especially the anterior end of the *Trachyteuthis*-gladius is completely different from *Libanoteuthis*. Instead, close affinities to *Glyphiteuthis* should be discussed. Re-investigations of specimens of *Glyphiteuthis ornata* (specimens of *G. minor* are considered to be juveniles of *G. ornata*) and specimens of "*Libanoteuthis" libanotica* yielded equal gladius proportions. In the Turonian specimens it seems that the median ridge is more developed than in Cenomanian specimens. However, this is possibly due to the flattened specimens of the Lebanese "fish beds" in comparison to a 3-dimensional preservation in the Bílá Hora Formation (Bohemia). In any case, there are only few arguments for separating specimens of *Glyphiteuthis* and *Libanoteuthis* in different genera. Therefore *Libanoteuthis* should be considered as a junior synonym of *Glyphiteuthis*.

Assigned species: *Glyphiteuthis ornata* (= *minor*?), *G. libanotica* and *G. boutillieri*.

Glyphiteuthis (= *Libanoteuthis*) *libanotica* Fraas, 1878 (Pl. VIII, Figs. A-B; Pl. IX)

1878 *Geoteuthis libanotica* – Fraas, p. 345, Pl. 6, Fig. 3.
1896 *Geoteuthis libanoticus* – Woodward, p. 231.
1920 *Geoteuthis libanotica* Fraas – Bülow-Trummer, p. 255.
1922 *Trachyteuthis libanotica* (Fraas, 1878) – Naef, p. 140, Fig. 49b.
1942 *Libanoteuthis libanotica* Fraas – Kretzoi, p. 125, Fig. 1.12, p. 134.
?1946 *Geoteuthis sahel-alma* (Fraas) (Naef) – Roger, p. 16, Fig. 9.
1946 *Trachyteuthis libanotica* (Fraas) – Roger, p. 17, Fig. 10.
1952 *Libanoteuthis libanotica* Fraas – Roger, p. 740.
1962 *Libanoteuthis libanotica* (Fraas) – Rioult, p. 11, Fig. 1b.
1966 *Trachyteuthis (Libanoteuthis) libanotica* Kretzoi, 1942 – Jeletzky, p. 45.
1977 *Trachyteuthis libanotica* (Fraas) – Donovan, p. 32.
1986 *Libanoteuthis libanotica* (Fraas, 1878) – Engeser & Reitner, p. 7, Fig. 2, Pl. 2, Figs. 1, 2.
1988 *Libanoteuthis libanotica* (Fraas, 1878) – Engeser, p. 69.

Holotype: Fraas (1878: Pl. VIII, Fig. B), Staatliches Museum für Naturkunde, Stuttgart (SMNS 26271).
Locus typicus: Hâqel, Lebanon.
Stratum typicum: Upper Cenomanian.
Geographic and stratigraphic distribution: Upper Cenomanian of Hâqel and Hjoûla, Upper Santonian of Sâhel Aalma, (Lebanon).
For a long time *Glyphiteuthis libanotica* has been known only from Hâqel, but Engeser & Reitner (1986: 9) considered the possibility that Naef (1922) mistook the localities of his specimens from the Noetling collection (Noetling, 1886), which were believed to derive from Sâhel Aalma. This implies that this genus occurs up to the Santonian.

Material: eighteen specimens identified as *Glyphiteuthis libanotica* belong to the MSNM-collection and were investigated: MSNM i25138 (Pl. IX, Fig. A), i24801 (Pl. IX, Fig. B), i25127 (Pl. VIII, Fig. A), i24959, i20589, i24957, i20588, i20857a+b, i25136, i25130, i12599, i25137, i25131a+b, i24958, i23434, i25129, i26734, i23422. Except MSNM i2480, which comes from Hjoûla, all specimens originate from Hâqel.

Description

Gladius: dimensions of eight dorsoventrally embedded specimens are completely preserved and are therefore available for comparative measurements (Fig. 8).
With gladius lengths of 4-8 cm, all measured specimens are small compared to *Glyphiteuthis ornata* and *Trachyteuthis*. Lateral field length (lfl) is between 1.4–3.4 cm. The ratio of lateral field length to gladius length (lfl/gl) varies slightly between 0.36–0.4. Maximum width of the lateral field (lfwmax) is between 1.3–2.6 cm. In cross-section the lateral fields are almost hemi-circular. The ratio maximum lateral field width to lateral field length is between 0.9–1. Especially specimen MSNM i25127 exhibits a precise gladius outline (Pl. VIII, Fig. A). This specimen clearly shows a sharply pointed anterior end as well as a slight lateral constriction in the anterior third of the gladius.
In specimens MSNM i25130, i24958 and i24959 an indistinct but prominent median ridge or even keel ("Mittellinie" of Engeser & Reitner (1986: 7) is present. In contrast
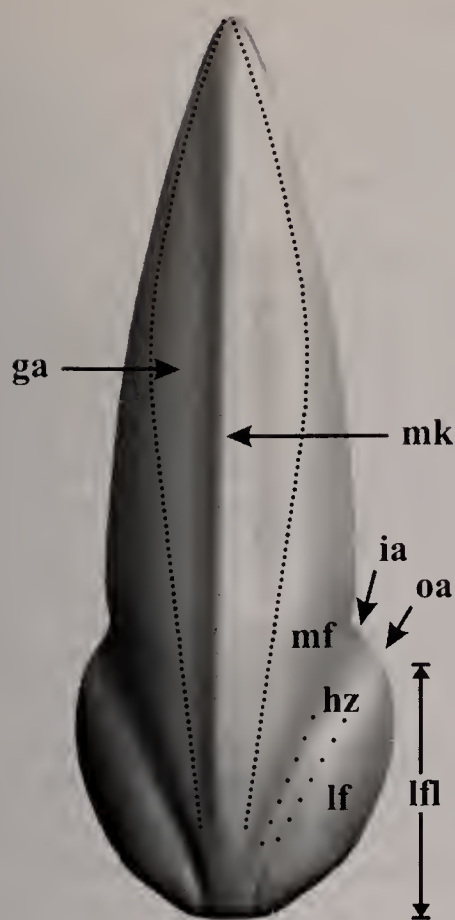
Fig. 8 - *Glyphiteuthis* (= *Libanoteuthis*) *libanotica*. Reconstruction of the gladius. ga= granulated area; hz = hyperbolar zone; ia = inner asymptote; lf = lateral field; lfl = lateral field length; mf = median field; mk = median keel; oa = outer asymptote.

to observations by Engeser & Reitner (1986) the median ridge runs continuously from posterior to anterior. After re-investigation of the Holotype of *Glyphiteuthis libanotica* it must be assumed that the lack of a posterior median ridge in this specimen is due to incomplete preservation.

MSNM i24959 displays dorsal imprints of granulations. In this specimen one row of coarse granules is visible along the median ridge. Smoother granules flank the median ridge on both sides. Additional ridges similar to those assumed in *Trachyteuthis* cf. *hastiformis* (see above) strictly delimit the granulation. They diverge with an angle of 20°. As in *Trachyteuthis* cf. *hastiformis* it seems that the granulated area in MSNM i25138 is slightly elevated above the rest of the gladius surface (Pl. IX, Fig. A). In the middle part of the gladius the ridges become indistinct and the granulation broadens. In the anterior third of the gladius it almost reaches the marginal edges (MSNM i20589).

Preservation of growth lines is weak (MSNM i25138). In some specimens imprints of growth lines are preserved (MSNM i24958). It seems that growth lines have a weak curvature, and so the hyperbolar zone is indistinct. Inner and outer asymptotes are therefore imaginary.

Arms: in at least ten specimens (MSNM i24957, i24958, i25129, i25131a+b, i24959, i24801, i25130, i25138, i20587a+b, i12599) arms are more or less preserved as outstanding discolorations. Phosphatised arm musculature is only preserved in MSNM i20875 but counting has proved to be difficult. Although a complete arm crown is absent, each specimen suggests that these animals had relatively long and slender arms (Pl. IX, Fig. B). Average arm thickness is 0.2 mm. Absolute arm length could not be determined. Tentacles or tentacle clubs are never present.

Suckers: few imprints of suckers are discernible in specimen MSNM i25130. It is not possible to determine the position of suckers (for instance, if they are arranged in one, two or more rows). Presumably they form distal suckers. They are almost 1 mm in diameter and radial in shape. Cirri are never observed.

Head: in each specimen where remains of arms are visible remains of the head can be assumed by the position of the buccal mass.

At least two specimens (MSNM i12599, in ventral view and i24801, in lateral view) exhibit a circular whitish structure in the head region, strongly phosphatising under ultraviolet light (Pl. IX, Figs. B-C). This structure is determined as the muscular buccal mass. In both cases it almost touches the anterior end of the gladius. This might indicate a retractable head. Other specimens confirm this assumption. However, it can not be decided if the head was clearly demarcated.

Beaks: beaks occur in several specimens but provide no information about their detailed morphology owing to strong compaction.

Fins: absolutely no indications about fin morphology are present, neither in specimens of this collection nor in specimens from other collections.

Remarks: as mentioned above the ratio lateral field length to gladius length (lfl/gl) varies between 0.36–0.40. The Holotype of *Glyphiteuthis libanotica* was measured by the author and the lfl/gl-ratio of 0.38 from the Holotype fits well into this range. It must be emphasised that measurements of flattened (originally 3-dimensional) structures always contain errors because the rates of flattening usually differ. Nevertheless, at least one dorsoventrally flattened specimen (MSNM i25131) with a lateral field length to gladius length ratio (lfl/gl) of 0.3 gives the impression that probably two morphotypes occur. Though this cannot be statistically proved, it seems that there is 1) a stouter form with circa 38% and 2) a more slender form with lateral field length of circa 30% of the gladius length. Possibly arm length is a second distinguishing character, but present specimens do not provide sufficient information. Additional gladii with well-preserved soft-parts are therefore necessary.

Differential diagnosis: according to Engeser & Reitner (1986) co-existing *G. boutillieri* differ from *G. libanotica* by a solid median ridge and a specific median field. As shown above in *G. libanotica* the median ridge is continuous, too. Judging from the drawings of Lennier (1886) and Rioult (1962) likewise no difference concerning the median field is recognizable. Riegraf (1987) takes into consideration that *G. libanotica* is a junior synonym of *G. boutillieri*. In order to define specific differences between these two forms a re-investigation of the Holotype of *G. boutillieri* is necessary.

G. ornata possesses a ribbed median keel especially in the anterior third of the gladius (Kostak, 2002). In *G. libanotica* we have found no indications for ribs.

PHYLOGENETIC IMPLICATIONS

Since evidences for a close affiliation of fossil gladii with recent *Vampyroteuthis* and octopods have accumulated in recent decades (Bandel & Leich, 1986; Haas, 2002; Donovan *et al.*, 2003; Bizikov, 2004; Fuchs, 2006), "fossil teuthids" are unknown in the fossil record.

According to Engeser & Reitner (1986), Bandel & Leich (1986) and Engeser (1988) Prototeuthina, Loligosepiina and Teudopsidina (= Mesoteuthina) represent stem-lineage representatives of the Vampyromorpha. In contrast Haas (2002) considers them as stem-lineage representatives of all Vampyropoda. Bizikov (2004) assumes that the Loligosepiina are the stem group of the Vampyropoda and that teudopsid forms are stem-lineage representatives of the Octobrachia.

However, on the basis of hundreds of vampyropod gladii from different localities and stratigraphic levels a comparative study suggests that only the Prototeuthina (*Paraplesioteuthis, Plesioteuthis, Dorateuthis)* should be regarded as stem-lineage representatives of the Vampyropoda (Fuchs, 2006). Most probably the ventrally opened conus of the Loligosepiina and the Teudopsidina is a derivation of a closed conus (as in *Paraplesioteuthis* and *Plesioteuthis*) inherited from a phragmoteuthid ancestor (Fig. 9).

Compared to the Loligosepiina, Teudopsidina show a general tendency to reduce their median fields (Haas, 2002; Bizikov, 2004). Since the gladius rudiments of incirrate octopods (*Palaeoctopus newboldi*) are proved to be the result of a progressive reduction of the median field, Teudopsidina should indeed be considered as stem-lineage representatives of the Octobrachia.

Recent *Vampyroteuthis infernalis* exhibits gladius characteristics that can easily be derived from a loligosepiid gladius, which is why Loligosepiina are believed to be the stem group of the Vampyromorpha (Fuchs, 2006).

It must be pointed out that the Lithographic Limestones of Hâqel, Hjoûla and Sâhel Aalma apparently do not contain unambiguous representatives of the Decabrachia despite its extraordinary preservational potential.
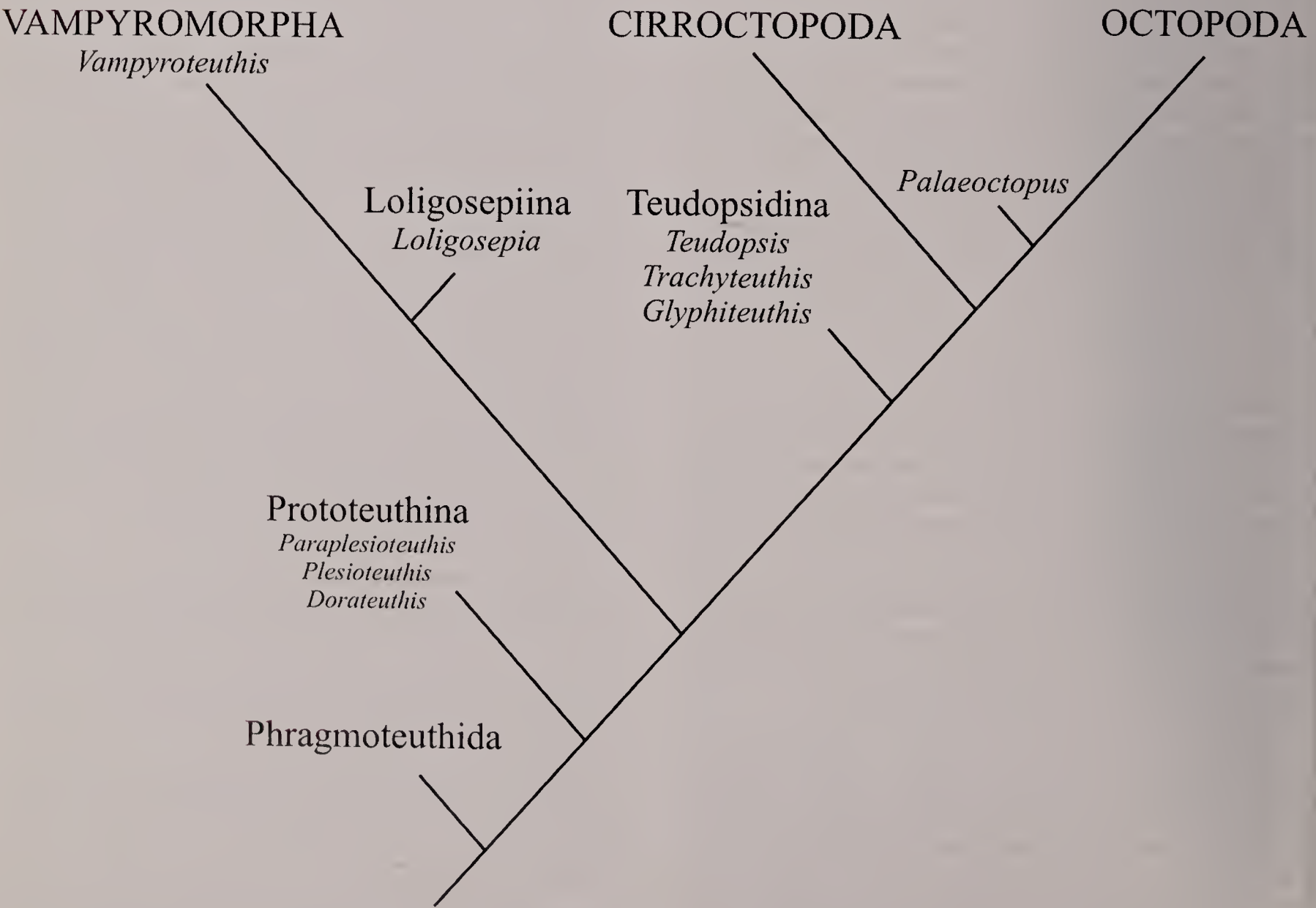
Fig. 9 - Basic phylogeny of the Vampyropoda.

CONCLUSIONS

Although well-preserved coleoids from Lebanon were already praised during the nineteenth century, previous information about diversity and morphology was scarce. The great number of Lebanese coleoids enables to enlarge the diversity up to six species (*Acanthoteuthis syriaca, Palaeoctopus newboldi, Dorateuthis syriaca, Rachiteuthis donovani, Trachyteuthis* cf. *hastiformis, Glyphiteuthis libanotica*) and to increase the morphological understanding of most of them.

Hâqel, Hjoûla, and Sâhel Aalma exhibit a vampyropod diversity that consists of a mixture of conservative and modified species. Especially the discovery of *Trachyteuthis* demonstrates a remarkable evolutionary stability within this genus from the Jurassic up to the Late Cretaceous. *Glyphiteuthis* displays only a slight modification of a typical teudopsid gladius.

The gladius of *Rachiteuthis* can be seen as a modification of a palaeololiginid gladius. Whereas the posterior part of the gladius with its lateral fields is more or less unmodified the rachis-like median field is strongly elongated compared to *Palaeololigo*.

The gladius of *Dorateuthis* must be considered as a moderate modification, which derived from a *Plesioteuthis*-like gladius. *Plesioteuthis* possesses a reduced but ventrally closed conus with short lateral fields. The median field is comparatively narrow but well developed. In *Dorateuthis*, in contrast, the median field seems to be only membranous with a very poor preservational potential. In this way the sturdy lateral ridges exclusively provide for the construction of the gladius and thus for the longitudinal rigidity of the mantle cavity. Morphological knowledge about the conus of *Dorateuthis* is poor, but it seems that it is distinctly reduced.

Except in extraordinary Konservat-Lagerstätten such as Christian Malford, Holzmaden, Solnhofen and Lebanon, coleoid records are often sporadic (except belemnite rostra). Owing to bad preservational conditions, morphological comparisons between fragmentary specimens are usually problematic. This remarkable coleoid collection from Hâqel stored in the Museo di Civico di Storia Naturale di Milano demonstrates the advantages and especially the importance of a sufficient number of specimens in order to verify earlier assumptions and to present a reliable morphological and taxonomical evaluation.

Unfortunately, an adequate Konservat-Lagerstätte is missing between the "evolutive windows" Solnhofen (Tithonian) and Sâhel Aalma (Santonian). Sâhel Aalma forms the last "evolutive window" in the earth history for we do not have any Konservat-Lagerstätte containing coleoids during the Cenozoic (coleoids are apparently unknown in Monte Bolca). Present results demonstrate the enormous significance of Hâqel, Hjoûla, and Sâhel Aalma for the reconstruction of the evolutionary history of vampyropods. Interestingly, no information about coleoids from Nâmmoura is available.

Most probably, present contributions are preliminary, because additional information about Lebanese coleoids is expected from another 80 specimens housed in the Black Hills Museum of Natural History in Hill City (South Dakota, USA).

Acknowledgments

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Morphology, taxonomy and diversity of vampyropod Coleoids (Cephalopoda) from the Upper Cretaceous of Lebanon
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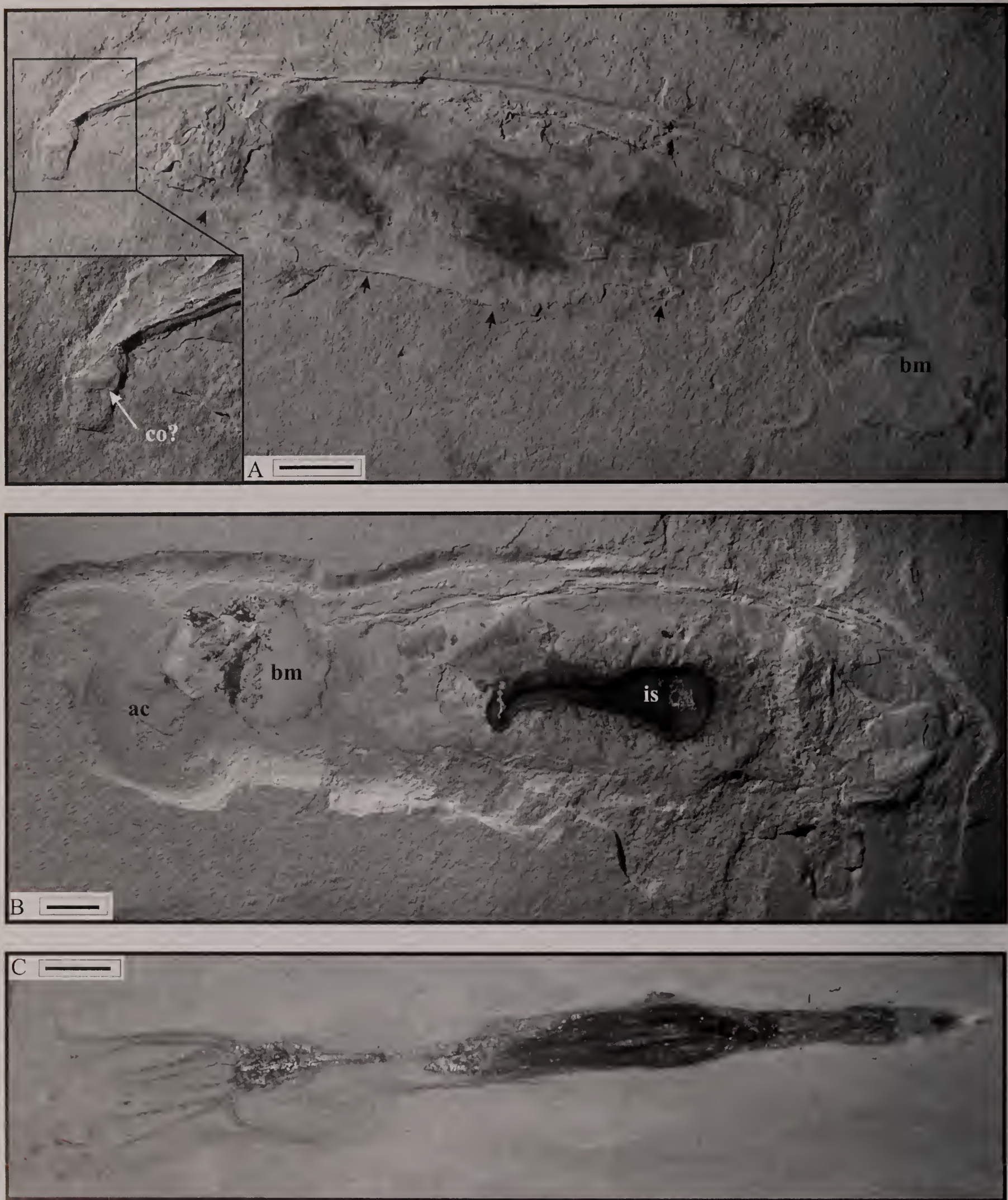
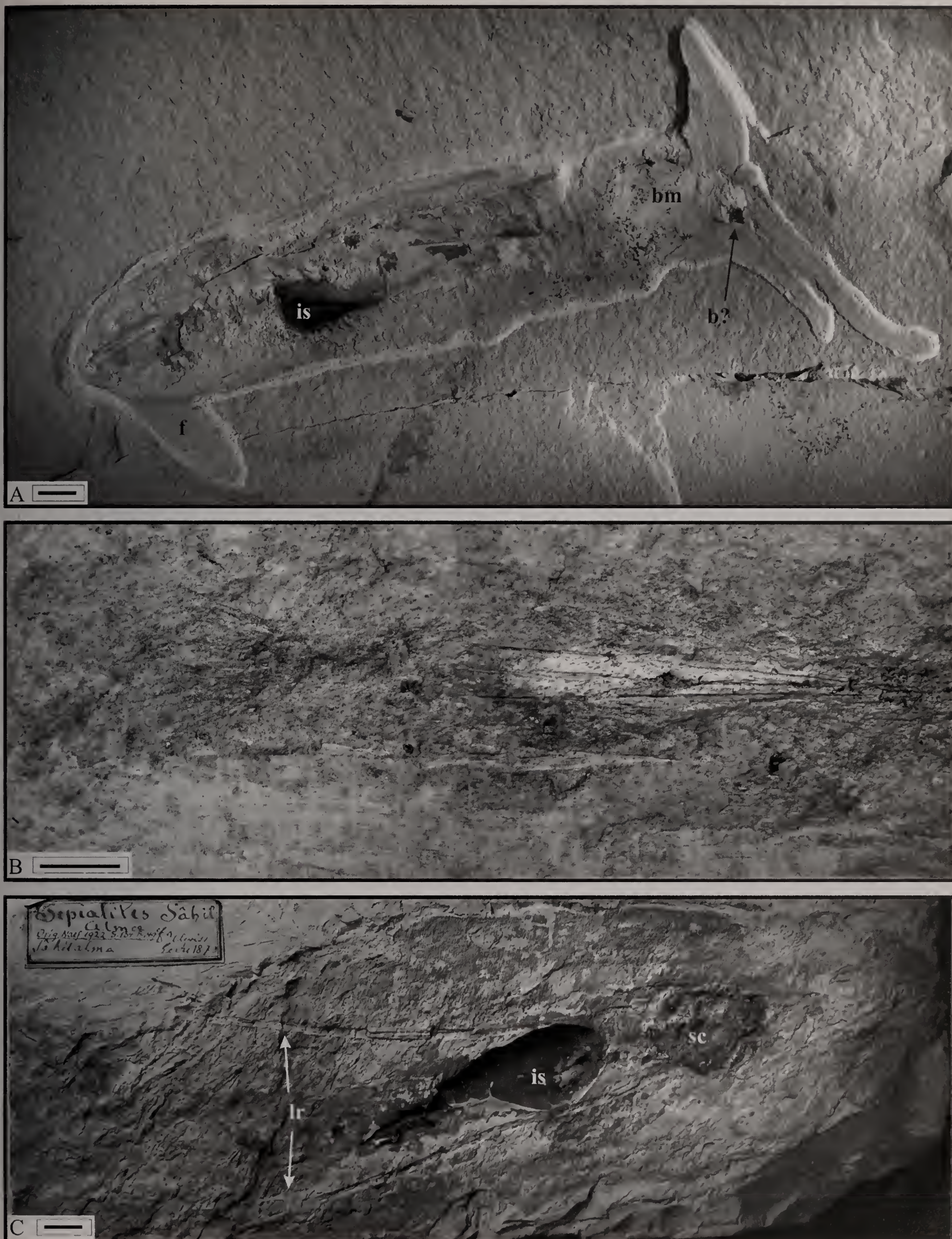
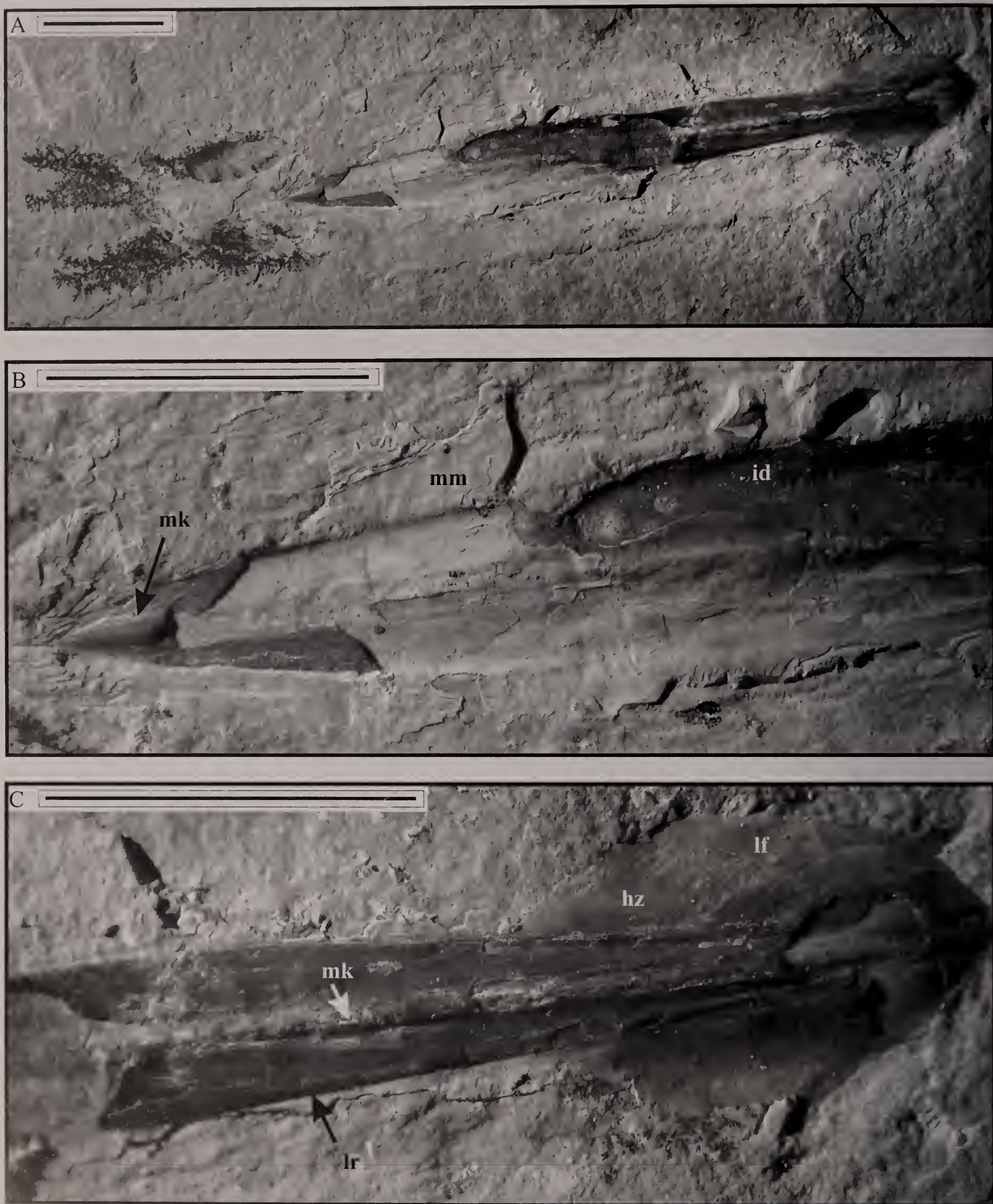
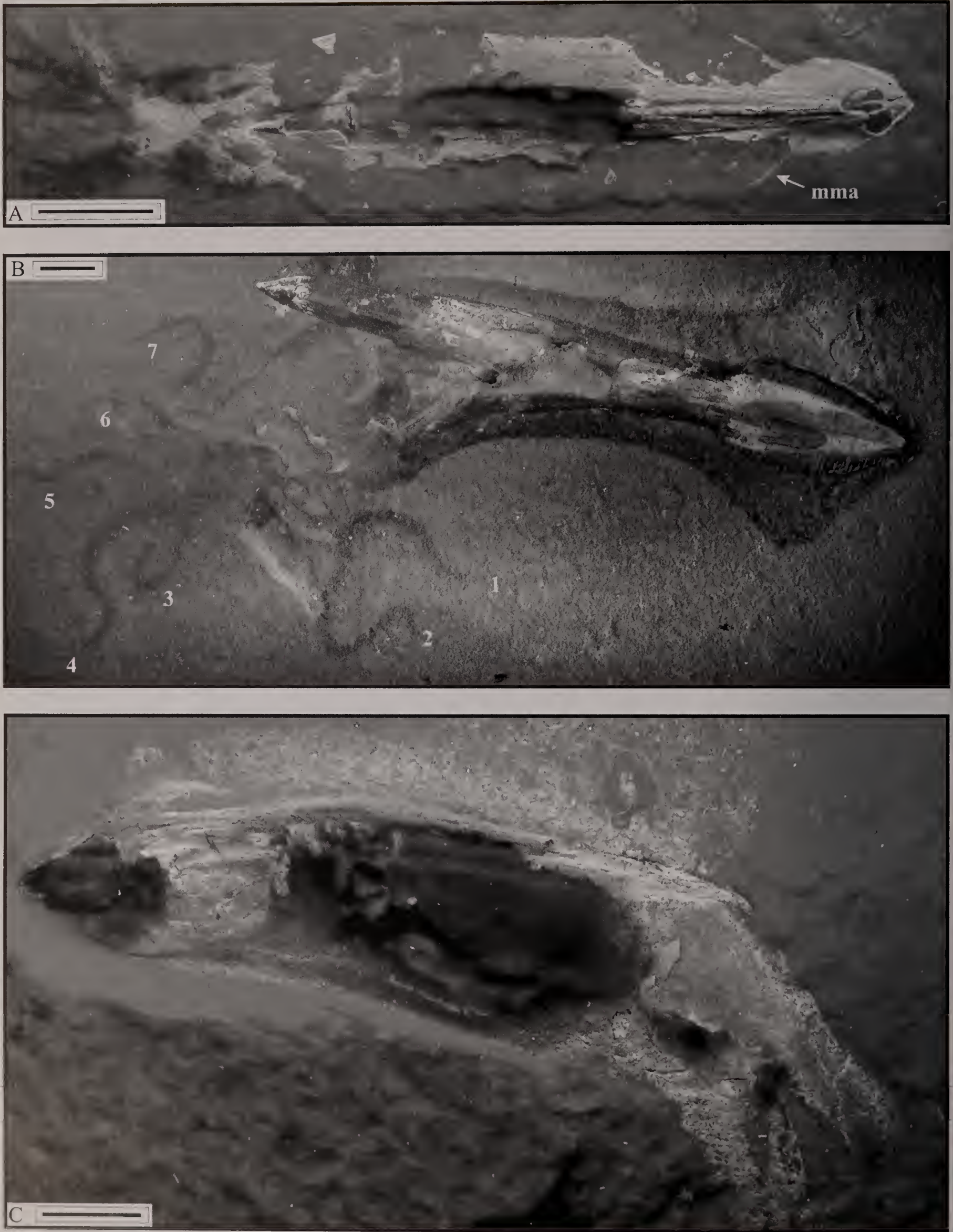
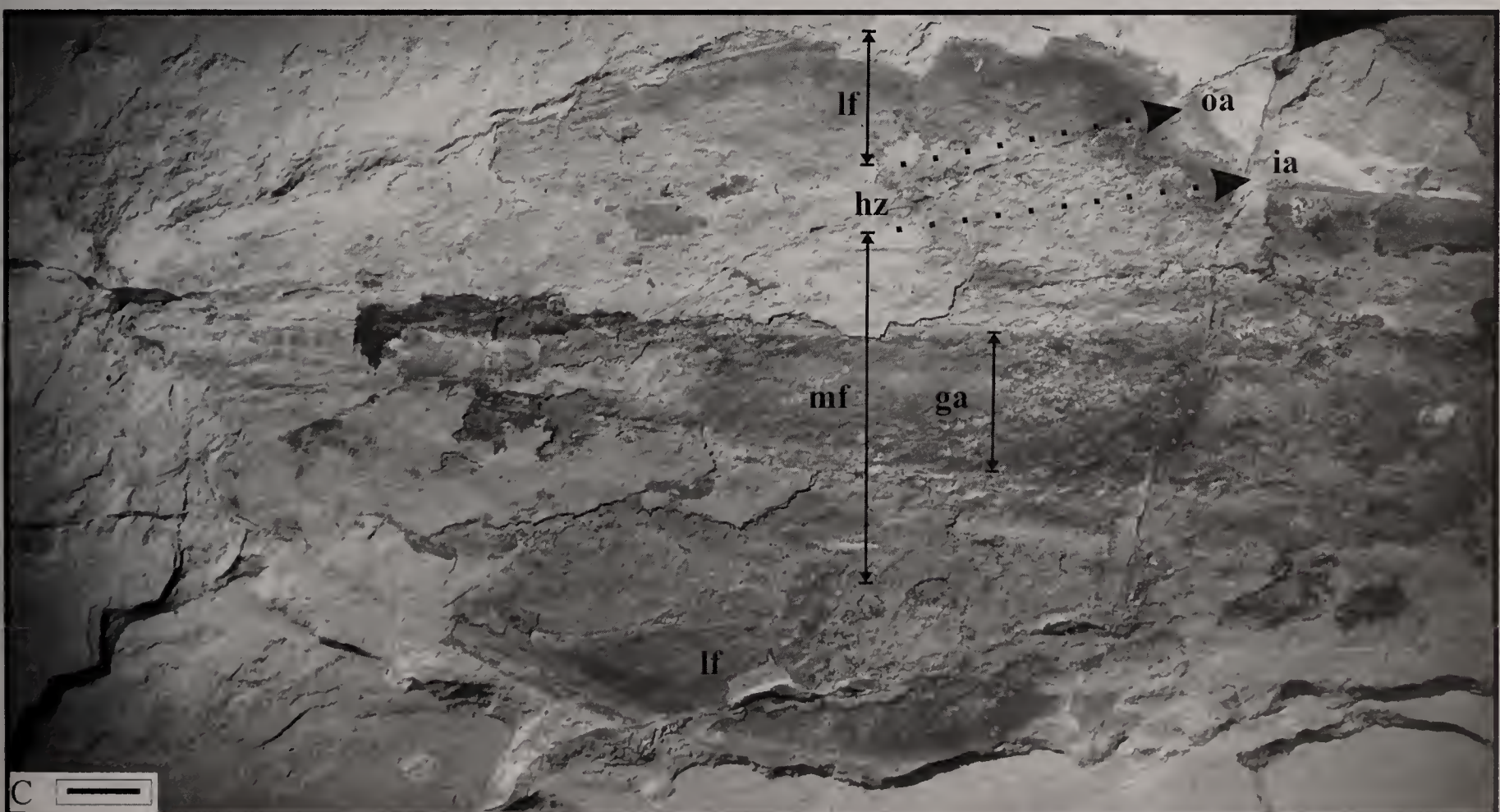
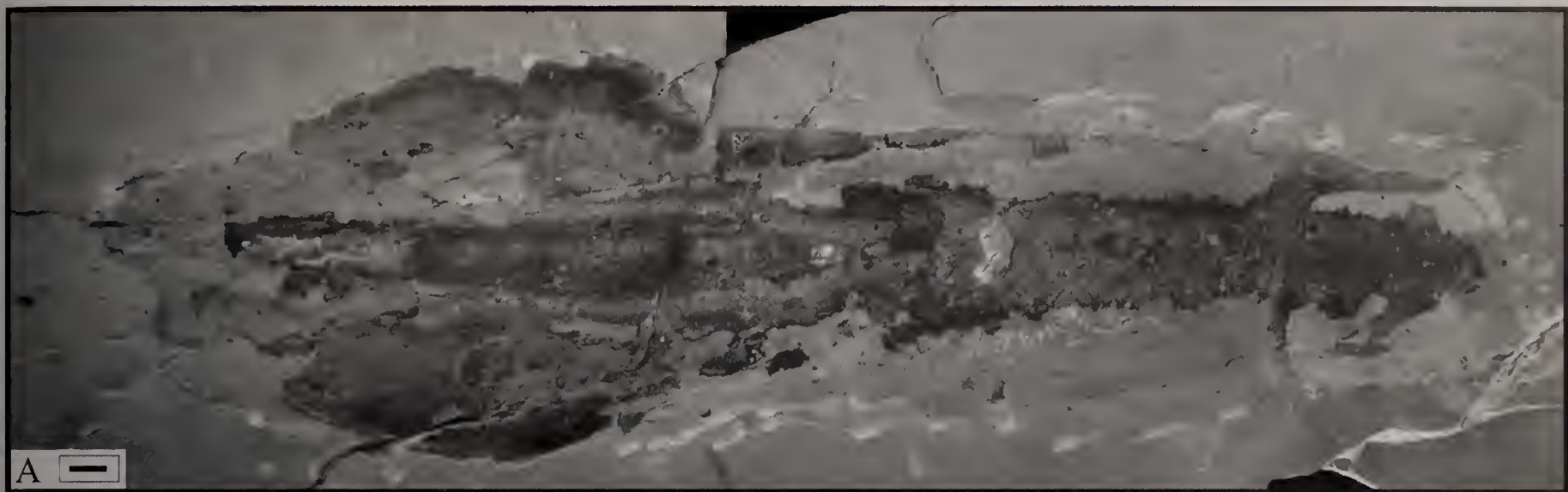
Volume XXXIV – Fascicolo II

Pl. I - *Dorateuthis syriaca.* A) Specimen MSNM i25144 from Hjoûla. Seen in ventral view. is = ink sac; lr = lateral ridge; sc = stomach contents. Scale bar: 1 cm. B) Same specimen as in Fig. A. Close up of the posterior region. Punctuated line marks supposed lateral fields (lf); lr = lateral ridge. Scale bar: 1 cm. C) Specimen MSNM i23108 from Sâhel Aalma. Seen in ventral view. lr = lateral ridge; mf = median field; mm = mantle musculature; mr = median ridge. Scale bar: 1 cm.

Pl. 11 - *Dorateuthis syriaca*. A) Specimen MSNM i24800 from Hjoûla. Seen in lateral view. bm = buccal mass; co = conus. Arrow heads mark and delimit the outline of the ventral mantle. Scale bar: 1 cm. B) Specimen MSNM i25133 from Hjoûla. Seen in lateral view. ac = arm crown; bm = buccal mass; is = ink sac. Scale bar: 1 cm. C) A specimen from Sâhel Aalma deposited in the Naturhistorisches Museum Wien, NHMW 1998z0105/0000 (original of Lukeneder & Harzhauser 2004). Seen in ventral view. The arm crown consists of eight arms. Note, that thickness of arms, body as well as gladius outline is a preparational artefact. Scale bar: 1 cm.

Pl. III - *Dorateuthis syriaca.* A) Specimen MSNM i25134 from Hjoûla. Seen in lateral view. b = beaks; bm = buccal mass; f = fin; is = ink sac. Scale bar: 1 cm. B) Holotype of *Dorateuthis syriaca* from Sâhel Aalma (British Museum of Natural History London, BMNH C5017). On the left a weak arm crown is visible. On the right weak imprints of the gladius with lateral and median ridges. Scale bar: 1 cm. C) Holotype of *Dorateuthis sahilalmae* from Sâhel Aalma (Staatliches Museum für Naturkunde Stuttgart, SMNS 26269). Seen in dorsal view. Lateral ridges (lr) diverge at a remarkable apikal angle. Most probably this due to a longitudinal disrupted gladius. is = ink sac. Scale bar: 1 cm.

Pl. IV - *Rachiteuthis donovani* (*nov. spec.*). A) Holotype (MSNM i25142) from Hjoûla. Seen in dorsal view. Scale bar: 1 cm. B) Same specimen as in Fig. A. Close up of the anterior part of the gladius. Where parts of the gladius have not been preserved, imprints of the ventral side are visible. id = ink duct; mk = median keel; mm = muscular mantle. Scale bar: 1 cm. C) Same specimen as in Fig. A. Close up of the posterior part of the gladius. hz = hyperbolar zone; lf = lateral field; lr = lateral ridge; mk = median keel. Scale bar: 1 cm.

Pl. V - *Rachiteuthis donovani* (*nov. spec.*). A) Paratype I (MSNM i25135) from Hjoûla. The gladius is seen in dorsal view, whereas the body is in lateral aspect. ac = arm crown; bm = buccal mass; f = fin; fu = funnel; is = ink sac. Scale bar: 1 cm. B) Paratype II (MSNM i25139) from Hjoûla. Gladius in dorsal view. Body in lateral view. is = ink sac. Scale bar: 1 cm. Left bottom corner: a close up of the head region. It seems as if the dorsal mantle is fused with the head region.

Pl. VI - *Rachiteuthis donovani* (*nov. spec.*) photographed with ultra violet light. A) Holotype. Phosphatised remains are shining white. mma = posterior mantle margin. Scale bar: 1 cm. B) Paratype I. Although tissues are poorly posphatised, number of arms (1-8), body as well as fin outlines are distinctive. Scale bar: 1 cm. C) Paratype II. At least four arm stubs are visible. Scale bar: 1 cm.

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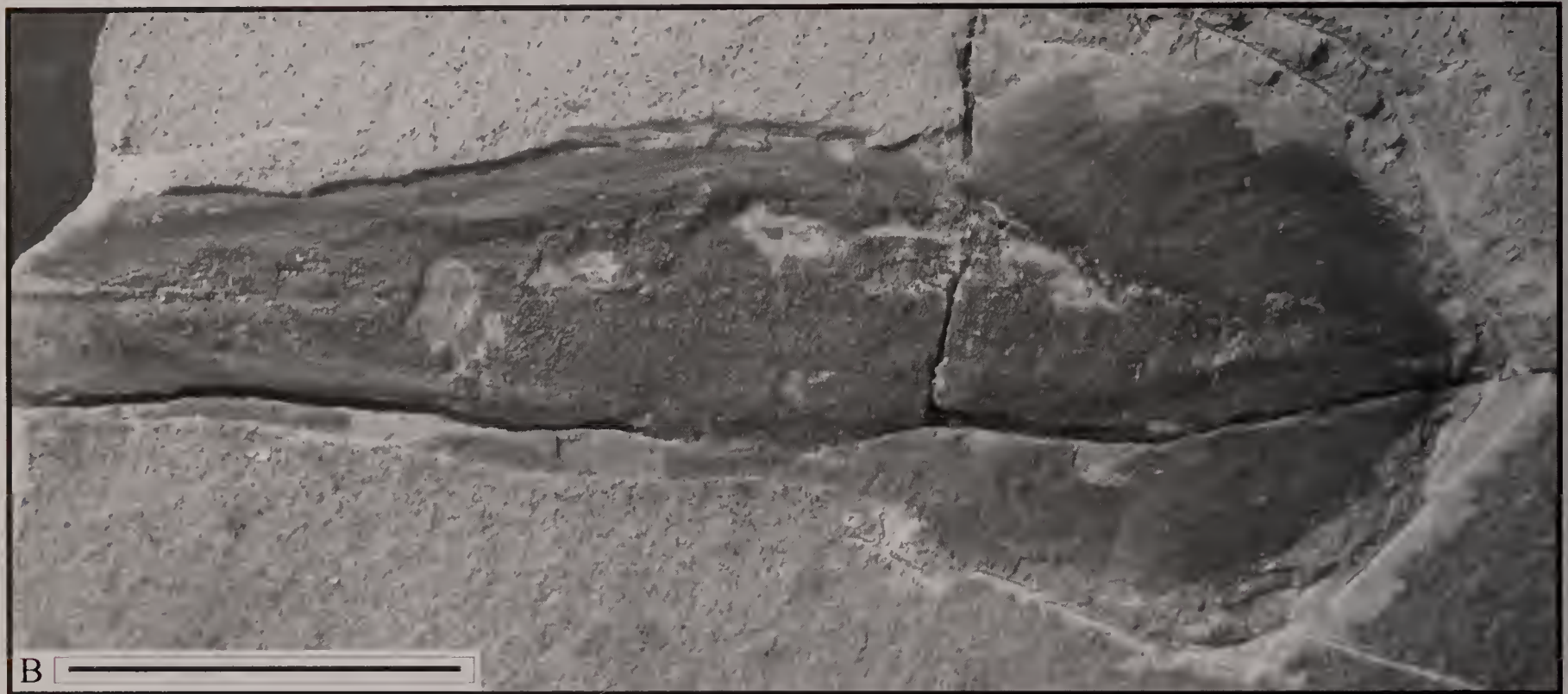
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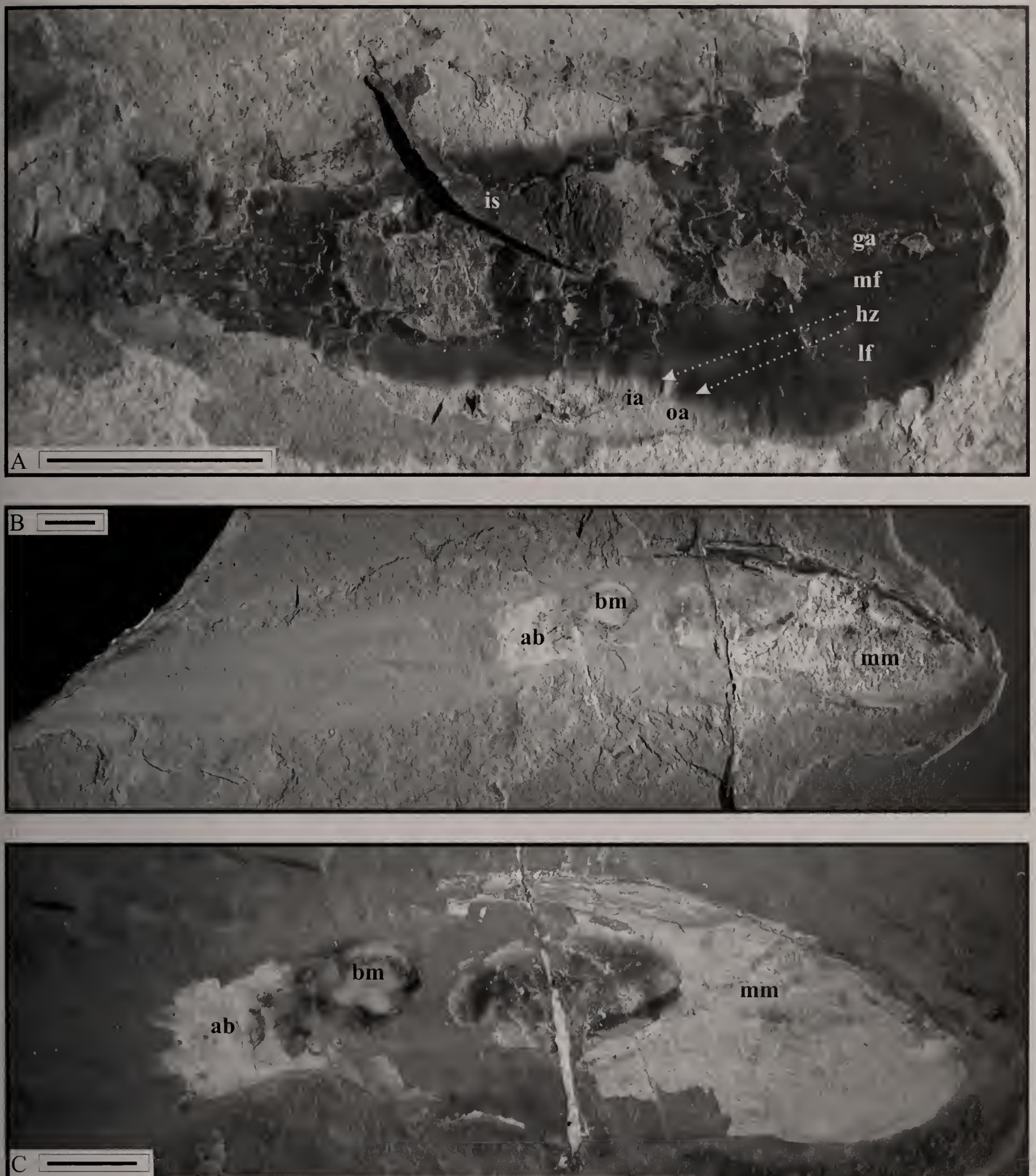
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MICHAEL W. CALDWELL

A NEW SPECIES OF *PONTOSAURUS* (SQUAMATA, PYTHONOMORPHA) FROM THE UPPER CRETACEOUS OF LEBANON AND A PHYLOGENETIC ANALYSIS OF PYTHONOMORPHA

MILANO LUGLIO 2006

Elenco delle Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano

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In copertina: *Pontosaurus kornhuberi*. Watercolour by Fabio Fogliazza.

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Michael W. Caldwell

A new species of *Pontosaurus* (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a phylogenetic analysis of Pythonomorpha

Abstract - A new fossil marine squamate from the Upper Cretaceous (Cenomanian) of Lebanon is described and its phylogenetic relationships analyzed. The taxon represents a new species of *Pontosaurus*, previously known from only the type species and only one specimen, designated *Pontosaurus lesinensis* (Kornhuber, 1873). The new taxon is very well preserved including the squamation and a complete tail numbering 163 caudal vertebrae. New and important features of the braincase of pontosaurs are highlighted: 1) the supraoccipital position and its overlap of the parietal; 2) the alar process of prootics elongate contact with parietal; 3) the reduction of the paroccipital process. A phylogenetic analysis of pythonomorphs, utilizing these new characters in a data matrix of 77 characters and 10 terminal taxa, finds nine shortest trees with a tree length of 119 steps (C.I. = 0.773; HI = 0.226). The nine shortest trees vary only in the sistergroup relationships of *Aphanizocnemus libanensis* within non-mosasauroid pythonomorphs, and the ingroup relationships of ophidian pythonomorphs. For example, cladogram one presents the following sistergroup structure: ((Aigialosauridae, Mosasauridae) (Dolichosauridae (*Aphanizocnemus libanensis* ((*Pontosaurus lesinensis, Pontosaurus kornhuberi*) (*Adriosaurus suessi* (*Pachyophis woodwardi* (*Pachyrhachis problematicus,* Serpentes))))))). In the context of the hypothesized phylogeny presented in this study, the functional morphology of pontosaurs is discussed, highlighting tail and limb function in relationship to locomotory capability.

Key words - Squamates, pythonomorphs, marine lizards, Cretaceous, Lebanon, phylogeny.

Riassunto - Una nuova specie di *Pontosaurus* (Squamata, Pythonomorpha) dal Cretacico superiore del Libano e una analisi filogenetica dei Pythonomorpha.

Viene descritto un nuovo squamato fossile marino e ne vengono analizzate le relazioni filogenetiche. Il taxon rappresenta una nuova specie di *Pontosaurus*, genere di cui era precedentemente nota solamente la specie tipo, con un singolo esemplare, denominata *Pontosaurus lesinensis* (Kornhuber, 1873). Il nuovo esemplare qui descritto è molto ben conservato: la coda di 163 vertebre è completa e sono presenti resti delle squame. Vengono messe in luce nuove e importanti caratteristiche della scatola cranica: 1) la posizione del sopraoccipitale e la sua sovrapposizione al parietale; 2) l'esteso contatto del processo alare dei prootici con il parietale; 3) la riduzione del processo paraoccipitale. Una analisi filogenetica dei pitonomorfi che utilizza questi nuovi caratteri in una matrice di 77 caratteri e 10 taxa terminali produce nove alberi con una lunghezza di 119 steps (CI = 0.773; HI = 0.226). Questi nove alberi variano unicamente nelle relazioni filogenetiche di *Aphanizocnemus libanensis* entro i pitonomorfi non-mosasauroidi, e nelle relazioni filogenetiche interne dei pitonomorfi ofidi. Ad esempio il primo cladogramma presenta la seguente articolazione dei successivi sistergroups: ((Aigialosauridae, Mosasauridae) (Dolichosauridae (*Aphanizocnemus libanensis* ((*Pontosaurus lesinensis, Pontosaurus kornhuberi*) (*Adriosaurus suessi* (*Pachyophis woodwardi* (*Pachyrhachis problematicus,* Serpentes))))))). La morfologia funzionale dei pontosauri viene discussa nel contesto della filogenesi ipotizzata, evidenziando l'importante funzione locomotoria della coda e degli arti.

Parole chiave - Squamati, pitonomorfi, rettili marini, Cretacico, Libano, filogenesi.

INTRODUCTION

Over the course of their known history, encompassing more than 130 million years, squamate reptiles evolved a wide and surprising array of anatomies as the various clades radiated and adapted into both terrestrial and aquatic environments. For example, limb reduction to complete limblessness, usually associated with extreme increases in body length, is observed in almost all lineages of living squamates (Greer, 1991; Caldwell, 2003) and certainly characterizes the nearly 3,000 species of snakes, which are arboreal, terrestrial, fossorial, cryptic, and aquatic. Modern squamates also show an amazing range in size from the incredibly large komodo dragons to the smallest known living amniotes *Sphaerodactylus ariasae*, a Caribbean gecko, which is only 16 millimeters long (Hedges & Thomas, 2001).

The list of modern squamate adaptations and anatomical innovations allowing them to colonize varied environments is extensive with but two exceptions - the air and the sea. Among more than 7,000 species of living squamates, none have evolved powered flight though some do glide, and only 59 species have evolved and adapted to life in aquatic marine environments: one species of iguana, 50 species of true sea snakes, 5 species of sea kraits, and 3 species of file snakes.

Interestingly, while these living squamates show remarkable adaptations to life in marine environments, the true acme of squamate evolution in marine environments is not found among modern species, but rather among fossil squamates. It is the extinct pythonomorphs, i.e., the dolichosaurs, pontosaurs, aigialosaurs, mosasaurs, and

early snakes, which truly became "aquatic" in every sense nearly 100 million years ago. This aspect of squamate evolution and evolutionary history is very poorly detailed in the literature purporting to evaluate aspects of squamate evolution. For example, the recent and excellent treatise on lizard diversity and evolution by Pianka & Vitt (2003: 260) only uses the word "mosasaur" once in more than three hundred pages, and never even mentions the existence of aigialosaurs, dolichosaurs, pontosaurs, adriosaurs or coniasaurs. As a result, there is also no discussion of the extent of pythonomorph evolution and adaptation to marine environments. This knowledge vacuum can only be rectified by the presentation of synthetic works, fusing phylogeny, function, and anatomy, that detail these missing pieces of squamate evolutionary history.

This study presents a description and phylogenetic analysis of a new species of ancient marine squamate, assigned to the genus *Pontosaurus*, that was found in 95 million year old rocks (Upper Cretaceous) in Lebanon. This new specimen is remarkably complete, including the preservation of soft tissues, and thus permits a unusual degree of "biological" interpretation (Pl. 1). The genus *Pontosaurus* was previously based on only one specimen, GBA 1873/4/2 (GBA, Austrian Geological Survey, Wien, Austria), the type species, *Pontosaurus lesinensis* (Kornhuber, 1873). *Pontosaurus lesinensis* was found in rocks outcropping on the island of Hvar, Croatia (Pierce & Caldwell, 2004) that are considered to be chrono-equivalents of those in Lebanon that produced the new species described here.

The new specimen was collected from a quarry in the Valley of Al Gabour near Al Nammoura, 10 km southeast of Hadjula, Lebanon (Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999). Previous to this work, Dal Sasso & Pinna (1997) had described the first known lizard from the marine sediments of Lebanon, *Aphanizocnemus libanensis*, which is considered to be Middle Cenomanian in age and was collected at a third quarry near Hakel, Lebanon. The specimen described here is therefore the second known lizard from the platy limestones of Lebanon and is a very different animal compared to *A. libanensis*.

Recent work by Caldwell & Dal Sasso (2004) described the remarkably well-preserved squamation of the new lizard, a feature not usually preserved in vertebrate fossils and certainly not for squamates. In this study the squamation will be reviewed as part of the overall description of the specimen, but the focus will be on the osteology. Characters obtained from this study will be added to a modified version of the character matrix of Pierce & Caldwell (2004) for the purpose of constructing a phylogenetic hypothesis of all pythonomorphs.

PONTOSAURS, DOLICHOSAURS AND BASAL PYTHONOMORPHS: AN OVERVIEW

In 1873, Kornhuber described a new genus and species of Cretaceous lizard from two separate specimens preserved on platy limestone slabs that had come from quarries outcropping on the island of Hvar, Croatia, known in Italian as Isola di Lesina. Kornhuber's plate "A" preserved the posterior portion of the skeleton of a small reptile; this plate made its way to Vienna, Austria, by 1869. Kornhuber's second specimen, plate "B", arrived in Vienna in 1870 and preserved the anterior portion, including the head, neck and forelimbs, of a second small reptile. Kornhuber's comparison of the two specimens led him to conclude they were the same thing, if not the same individual, and he therefore assigned them to the same species, *Hydrosaurus lesinensis*; the genus *Hydrosaurus* (Wagler, 1830) is now recognized as the junior synonym of the extant monitor lizard genus, *Varanus* (Merrem, 1820).

In 1892, Gorjanovic-Kramberger renamed *Hydrosaurus lesinensis* as *Pontosaurus lesinensis* (Kramberger, 1892) based on his assessment that it was not similar enough to the extant *Varanus* (=*Hydrosaurus*) to warrant assignment to that genus. In the act of recognizing yet another fossil Adriatic lizard, including *Aigialosaurus dalmaticus* (Kramberger, 1892), *Adriosaurus suessi* (Seeley, 1881), and *Acteosaurus tomassinii* (Meyer, 1860), Kramberger created the Family Aigialosauridae to include all the fossil forms.

Nopcsa (1903) reevaluated the systematic position of *P. lesinensis* in a study that included all of Kramberger's (1892) taxa, as well as *Dolichosaurus longicollis* (Owen, 1850), *Opetiosaurus bucchichi* (Kornhuber, 1901), *Carsosaurus marchesetti* (Kornhuber, 1893), and *Mesoleptos zendrinii* (Cornalia, 1851). Nopcsa (1903) identified common features shared by *Pontosaurus*, *Acteosaurus*, *Adriosaurus* and *Dolichosaurus*, and assigned them all to the family Dolichosauridae (Gervais, 1852), while *Aigialosaurus*, *Opetiosaurus*, *Carsosaurus*, and *Mesoleptos* were assigned to the family Aigialosauridae.

Since Nopcsa (1903), except for brief mentions in comparative studies (Nopcsa, 1908, 1923; Calligaris, 1987/1988; Rieppel, 1988; Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999), *Pontosaurus* had never been reexamined in any detail until the study of Pierce & Caldwell (2004). The latter study attempted to assess Nopcsa's (1903) assignment of *Pontosaurus* to the Dolichosauridae based primarily on recent analyses of existing specimens of *Adriosaurus*, *Acteosaurus*, *Dolichosaurus* and *Coniasaurus* (Caldwell, 1999a, 1999b; Caldwell, 2000; Caldwell & Cooper, 1999; Lee & Caldwell, 2000; Caldwell & Lee, 2004).

Owen (1850) described two monotypic genera of marine lizards, *Dolichosaurus longicollis* and *Coniasaurus crassidens*, based on a number of specimens collected from the Lower Chalk (Cenomanian; Upper Cretaceous) of southeast England. *Dolichosaurus* was diagnosed by a uniquely high number of cervical and dorsal vertebrae while unique tooth characters diagnosed *Coniasaurus*; Owen did not identify any characters linking these two taxa. Nopcsa (1908) restudied Owen's specimens and added several new specimens to the list of known coni-

asaurs and dolichosaurs. Unfortunately for *Coniasaurus*, Owen (1850) had misidentified the tooth-bearing element of the type specimen (a maxilla) as a dentary leaving Nopcsa (1908) to build on this error by first, not finding the true type, and second, by identifying a pair of well-preserved dentaries as Owen's type specimen (see Caldwell & Cooper [1999] for the venue of the holotype and a redescription of the type material). Caldwell's (1999a) description of *Coniasaurus gracilodens* highlighted several notable differences with *C. crassidens* such as tooth shape, maxillary tooth number, and robustness of the maxilla (the maxilla of *C. crassidens* is much more elongate than that of *C. gracilodens*). Interestingly, all species assigned to *Coniasaurus* are known only from disarticulated skulls and isolated vertebral elements. In contrast, the type and referred specimens of *Dolichosaurus longicollis* are articulated postcranial skeletons with only one very fragmentary skull and no preserved teeth (Caldwell, 2000). Without consideration of pontosaurs, adriosaurs, or acteosaurs, coniasaurs and dolichosaurs have been thought to be nested within basal mosasauroids (mosasaurs and aigialosaurs) since Nopcsa, (1908), or recently, since Caldwell's (1999b) hypothesis that they are the sistergroup to mosasauroids. The difficulty in resolving the *Coniasaurus* - *Dolichosaurus* problem is that both taxa are represented by non-comparable data: *Dolichosaurus* is known from complete postcrania with little or no skull material, while both species of *Coniasaurus* are known from skulls and only a small number of disarticulated vertebrae.

Nopcsa's (1903) suggestion that pontosaurs, adriosaurs, acteosaurs, coniasaurs, and dolichosaurs might all be assigned to the Dolichosauridae, in association with recent studies proposing a sistergroup relationship between all these taxa and the mosasauroids (Caldwell, 1999b; Lee & Caldwell, 2000), highlight the phylogenetic importance of these animals in understanding the evolution of Mesozoic marine squamates. Recent work by Caldwell & Lee (1997), Lee & Caldwell (1998, 2000), and Caldwell (1999b), all of which examined the larger problem of squamate phylogeny, found Serpentes to be nested within a squamate clade including dolichosaurids and mosasauroids, a group referred to as the Pythonomorpha (see Cope's [1869] original diagnosis of this group as contrasted with Lee & Caldwell's [2000] slightly modified definition).

To date, the one hundred and fifty-five years of investigation on Cenomanian marine squamates has achieved the consensus view that the fossil forms (i.e., pontosaurs, adriosaurs, acteosaurs, coniasaurs, and dolichosaurs) are closely related to each other; there is also a reasonable degree of consensus that these squamates share a common ancestor with mosasaurids and aigialosaurids. However, as to the phylogenetic position of this larger group within squamates, and of snakes with any one group of squamates, there is no common agreement. For the purposes of this study, I will consider pontosaurs, adriosaurs, acteosaurs, coniasaurs, and dolichosaurs as informal generic groupings assigned to the Pythonomorpha; the Dolichosauridae, the conventional taxon for all these taxa, will be treated as including only *Dolichosaurus* and *Coniasaurus*.

SYSTEMATIC PALAEONTOLOGY

Reptilia Linnaeus, 1758
Squamata Oppel, 1811
Pythonomorpha Cope, 1869
Genus *Pontosaurus* Kramberger, 1892
Type Species: *Hydrosaurus lesinensis* Kornhuber, 1873

Pontosaurus lesinensis (Kornhuber, 1873)

Holotypus: GBA 1873/4/2 (GBA, Austrian Geological Survey, Wien, Austria): articulated cranial and postcranial remains of one individual; postcranium includes 12 articulated cervical vertebrae, 28 dorsal vertebrae, shoulder girdles, forelimbs, fragments of femur, and pelvic girdle.

Locus typicum: Hvar Island (= Isola di Lesina), 43°10'N, 16°30'E, Croatia; upper Cenomanian-upper Turonian (Upper Cretaceous).

Generic Diagnosis: Long, slender lizard possessing unique supraoccipital-parietal articulation, with supraoccipital resting on top of and forming w-shaped suture with parietal; elongation of all postdentary bones; 10-12 cervical vertebrae; hypapophyses with large, unfused peduncles on C2-C10; 26-28 dorsal vertebrae; fused scapulocoracoid with primary coracoid emargination.

Pontosaurus kornhuberi sp. nov.
(Figs. 1, 2, 3 A-B, 4-18)

Synonomy: cf. *Pontosaurus* sp. Caldwell & Dal Sasso, 2004.

Derivatio nominis: named in honour of Prof. A. Kornhuber in recognition of his contributions to the study of pythonomorph squamates.

Holotypus: MSNM V3662: complete, articulated skeleton of one individual (1,037 mm in length), including trachea, bronchi and squamation, preserved on platy limestone slab, housed in the Museo di Storia Naturale di Milano.

Diagnosis: Maxilla with large medially inflected premaxillary process; jugal with distinct posteroventral tuberosity; parietal with broad flat, medially expanded dorsal table extending onto parietal rami; frontal margin emarginated with no distinct nasal processes; 10-11 cervical vertebrae; 26 dorsal vertebrae; 2 pygal vertebrae; 163 caudal vertebrae; non-imbricated scales on cheek, imbricated scales on remainder of body.

Locus typicum: Quarry in the Valley of Al Gabour near Al Nammoura, 10 km southeast of Hadjula, Lebanon (Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999).

Fig. 1 - Holotype, *Pontosaurus kornhuberi*, MSNM V3662. A) Interpretative drawing; B) photo. Scale bar = 10 cm.

OSTEOLOGICAL DESCRIPTION

State of preservation

MSNM V3662 possesses a long (46 mm long), thin skull (18.6 mm wide) with large orbits (Figs. 1, 2, 3 A-B) and an elongated postorbital region. The skull is flattened and preserved in dorsal view, but was clearly compressed from the left as the left mandible is exposed in lateral view while the right has rotated medially underneath the dermatocranium; only the medial aspect of the right mandible is visible to the right of the parietal. Likewise, the left maxilla has shifted into lateral view, and is broken away; the right maxilla is preserved in dorsal view, but is crushed downwards so that the ascending process is compressed onto the maxillary shelf. The neck bears at least 10 and probably 11 cervical vertebrae with ribs, and a trachea extending to the third dorsal rib. The limbs are well developed, and the forelimb (65 mm long) is reduced in size relative to the rearlimb (98 mm long); the right forelimb is not well exposed but the left is well preserved and articulated. The rearlimbs are both well preserved and in articulation. There are 26 pachyostotic trunk vertebrae and ribs; pachyostosis is not evident in the sacral or caudal skeleton. The tail is exceptionally long (680 mm) and possesses 163 caudal vertebrae; the number of caudals is reduced by two from the 165 as reported by Caldwell & Dal Sasso (2004) due to the recognition in this study of two probable pygal vertebrae. The haemal spines are almost twice as long as the neural spines and articulate with distinct haemapophyses; transverse processes disappear at the 8^{th} caudal vertebra. Detailed preservation in this fine-grained limestone has preserved the squamation both as molds, casts, and in many places, the original material included tonal variation.

1 cm

Fig. 2 - *Pontosaurus kornhuberi*, MSNM V3662, detail of the skull.

Skull

The skull is represented by the premaxilla, right maxilla and partial left maxilla, fragments of the septomaxillae, vomers, and possibly nasals, partial right and left prefrontals, complete right and left jugals, the left postorbital, postfrontal, and squamosal, and fragments of the right-side series of the same, a well preserved frontal, and parietal, the supraoccipital, a well-preserved left exoccipital-opisthotic and fragments of the right, probable left and right prootics, a left quadrate with fragments of the right, a well preserved left dentary with teeth, a well preserved left surangular with a poorly exposed right surangular, left and right articulars (Figs. 2, and 3 A-B), and perhaps the quadrate ramus of the right pterygoid.

Premaxilla

The premaxilla is a single bone and is well preserved though broken into small fragments along the length of the premaxillary bar (Fig. 4 A-B). The anterior tooth-bearing portion of the premaxilla (Fig. 4 C-D) is a small median element that flares right and left to support two teeth on each side of the sagittal plane (Figs. 2, 3, and 4). At its anterior tip, it is broad and flat with a small space equivalent to the width of one tooth base separating the right and left pairs of teeth; the anterior extent of the bone is posteriorly deepened just enough to support the alveoli for the four teeth and immediately becomes constricted posterior to this point in order to form a long and thin narial bar similar to that of *Pontosaurus lesinensis* (Fig. 3 C-D) (Pierce & Caldwell, 2004).

The premaxilla and its internarial bar is much better preserved in MSNM V3662 than that of the type of *Pontosaurus lesinensis* (Fig. 3 A-D) and shows an important feature shared in common with *Coniasaurus gracilodens* Caldwell, 1999. On the right side of the premaxilla in MSNM V3662 there is a small, laterally positioned fossa or small platform that lies below the level of the internarial bar and immediately posterior to the tooth bearing portion of the bone (Fig. 4 C-D). Immediately lateral, and still in proximate articulation is a matching,
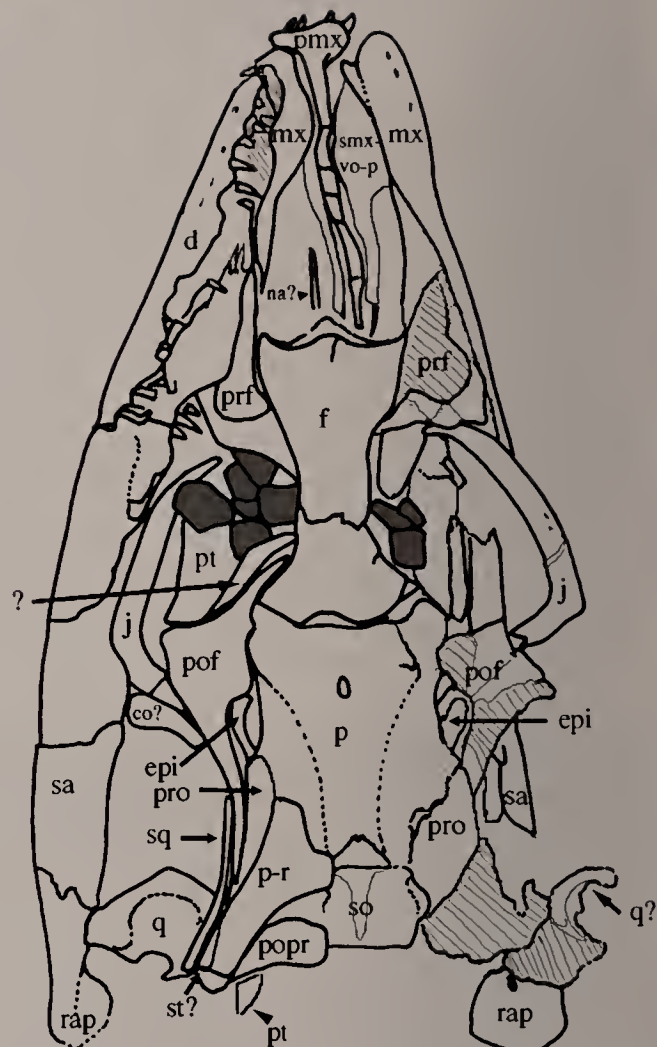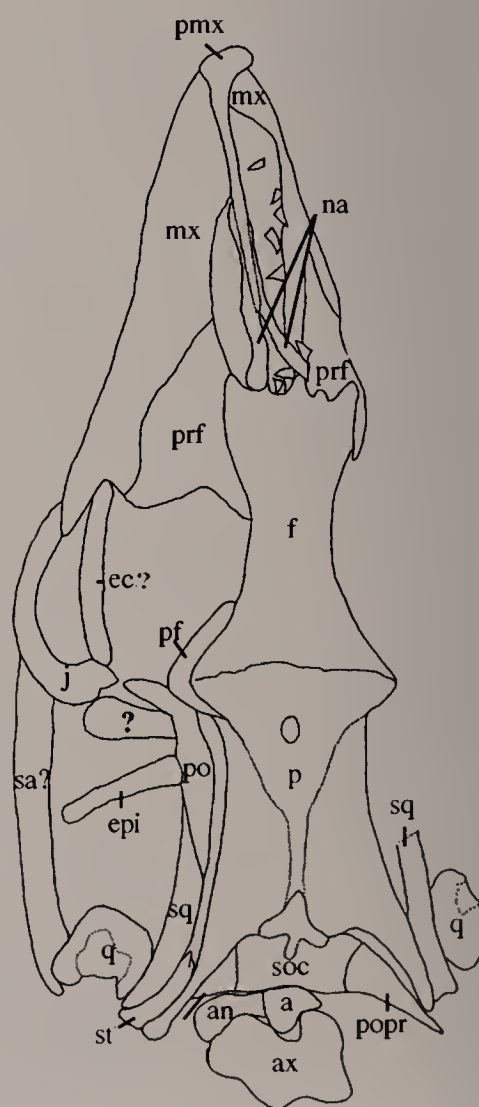
Fig. 3 - Skulls of *Pontosaurus kornhuberi* MSNM V3662 (A-B) and *Pontosaurus lesinensis* GBA 1873/4/2 (C-D). A) Dorsal surface of skull; B) line drawing of same; C) dorsal surface of skull; D) line drawing of same. Abbreviations: a, atlas intercentrum; an, atlas neural arch; ax, axis; co, coronoid; d, dentary; ec, ectopterygoid; epi, epipterygoid; f, frontal; j, jugal; mx, maxilla; na, nasal; p, parietal; p-r, parietal ramus; pf, postfrontal; pmx, premaxilla; pof, postorbitofrontal; po, postorbital; popr, paroccipital process of the exoccipital-opisthotic; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; rap, retroarticular process; smx-vo-p, septomaxilla and vomeropalatine; soc, supraoccipital; sq, squamosal; st, supratemporal; sa, surangular.
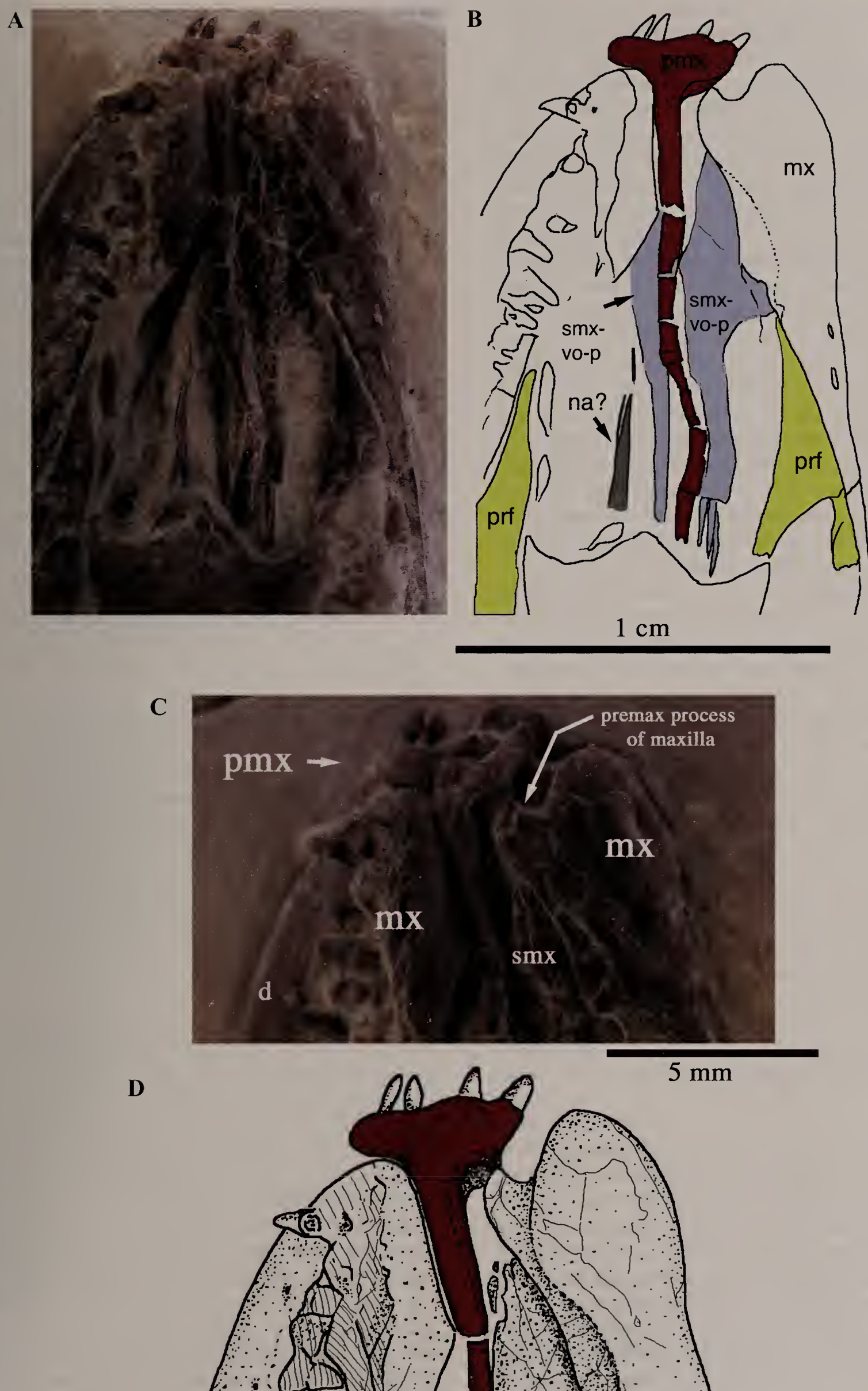
Fig. 4 - Snout of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of palatal elements viewed through external narial opening; B) line drawing with palatal and snout elements illustrated in color (premaxilla = red; septomaxilla and vomeropalatine = blue; prefrontal = yellow; possible nasal fragment = grey); C) photo detail of premaxilla showing right and left maxillae, premaxillary bar, and well preserved premaxillary process of right maxilla; D) line drawing of same with premaxilla highlighted in red. Abbreviations: see Fig. 3.

anteromedially directed hook-shaped process extending from the maxillary shelf of the right maxilla. The sidewall of the right maxilla is compressed on top of the maxillary shelf but the separation of the transverse shelf and vertical sidewall are still easily detected (Fig. 4 C-D).

The morphology and position of this anatomical feature is identical to that of *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 6 B, and 7 B). As was suggested by Caldwell (1999a), this process, likely a synapomorphy of *C. gracilodens* and *P. kornhuberi*, suggests that the very small premaxilla of the latter and by extension the probably equal sized premaxilla of the former, would have been mobile around these paired processes. The morphology of this anatomical feature hints at an unsuspected degree of premaxillary mobility in these small pythonomorph reptiles. The maxilla was not firmly sutured to the premaxilla, the premaxilla was long, and there is no evidence of a firm suture with the frontal at the posterior tip of the internarial bar. Similar snout kinesis is observed in modern snakes with the notable difference being the significantly shorter narial bar (Frazetta, 1970).

The internarial bar of *Pontosaurus kornhuberi* appears to bear a tiny notch at the posteriormost tip (Fig. 4 A-B); presumably, this notch contacted some portion of the internarial process of the frontal. It is not clear how firmly sutured this contact was, but it appears to have been rather loose. In contrast to *P. kornhuberi*, the internarial bar of *P. lesinensis* is sandwiched between a pair of nasal bones situated along its lateral borders that appear to restrict the premaxillary contribution to the external narial opening and seem to prevent its contact with the frontal bone, a scenario consistent with all squamates except mosasauroids (Fig. 3 C-D; Pierce & Caldwell, 2004). If nasals were present in *P. kornhuberi*, they are not well represented in MSNM V3662 by anything more than one possible sliver of bone lying in the left narial opening (Fig. 4 A-B). It is also possible that this fragment is a portion of the palatine and not the nasal. Further support for the absence of nasal bones is the different frontal margin morphology of *P. kornhuberi* as compared to *P. lesinensis* (the former is an effaced "w"-shape while the latter is a "w-w"-shape bearing two small nasal processes parasagittal to the internarial process [Fig. 3 C-D]).

Maxilla

The left maxilla is very poorly preserved and will not be described here. The right is much better preserved (Figs. 2, 3 A-B, 4) even though it is only visible in dorsal view; an accurate tooth count is therefore problematic. As described previously, the anterior tip of the maxilla is rounded and rises gently into a shallow but vertically oriented lateral wall that frames the margin of the narial opening (Fig. 4 A-B). Medial to the sidewall of the maxilla and near the anterior tip of the bone, is a well-developed premaxillary process that extends medially and anteriorly towards a fossa or recess on the premaxilla; the maxillary shelf, beginning immediately posterior to the premaxillary process, bears a scalloped margin lateral to its contact with the vomers. In dorsal view the anterior two-thirds of the maxilla shows an identical morphology to the maxilla of *Coniasaurus gracilodens* (Caldwell, 1999a). The difference between the maxillae of *P. kornhuberi* and *C. gracilodens* is the height and extent of the ascending process of the maxilla in the latter taxon. *Pontosaurus kornhuberi* possesses a low ascending process, similar to *P. lesinensis* (Fig. 3 A-D) and a fairly long anteriorly directed prefrontal that blocks any articulation between the frontal and maxilla. In *P. lesinensis* the ascending process is a long, low sloping feature of the maxilla that rises to form only about one half of the lateral margin of the narial opening (Fig. 3 C-D); a similar condition also characterizes *P. kornhuberi* except that the maxillary contribution to the narial opening is less, comprising about two fifths of the margin (Figs. 3 A-B, 4 A-B).

The posterior process of the maxilla extends below the orbit only far enough to contact the anterior tip of the jugal. However, this distance appears to be equal to about one half of the orbit diameter; a similar condition is observed in all mosasauroid pythonomorphs (Russell, 1967). Due to preservation and orientation of the element, it is not possible to determine how far posteriorly, and perhaps how far beneath the orbit, the dentition extended. In *Pontosaurus lesinensis* (Pierce & Caldwell, 2004), *Coniasaurus gracilodens* (Caldwell, 1999a) and *C. crassidens* (Caldwell & Cooper, 1999), the dentition terminates at the anterior margin of the orbit, as it does in other mosasauroids; it seems likely that the same condition exists in *P. kornhuberi*.

Although a maxillary tooth count is not possible, some aspects of the maxillary dentition are preserved on the left side of the skull and are worth describing. Most of the anterior teeth have been crushed and broken but some are well enough preserved so that their general outline can be observed: sharp slightly recurved piercing teeth set within a mass of ossified tissue as in other mosasauroids (Russell, 1967; Carroll & deBraga, 1992; deBraga & Carroll, 1993; Caldwell *et al.*, 2002); fluting similar to that observed in *Pontosaurus lesinensis* is not visible.

Septomaxilla

The septomaxillae are likely preserved in *Pontosaurus kornhuberi*, but it is not possible to differentiate the morphology of either the left or right element due to dorsal-ventral compaction of the bone on top of vomeropalatines (Fig. 4 A-B). Comparing the morphology of the anterior portion of the compressed septomaxilla/vomeropalatine mass to the probable septomaxilla of *Coniasaurus gracilodens* (Caldwell, 1999a, fig. 9), where the latter is shaped like an obtuse triangle with a tall, median crest paralleling the internarial bar indicates that the septomaxilla of *Pontosaurus kornhuberi* was similarly shaped and anteriorly located. However, it also must be remembered that this is not a certain identification but rather a discussion of the general similarities between these two taxa; by comparison, there are no preserved remnants of the septomaxillae in *Pontosaurus lesinensis* (Fig. 3 C-D).

Vomeropalatines

As with the septomaxilla, it is not possible, due to

preservational factors, to determine whether or not the vomers and palatines were separate bones. As it has been shown that the two elements are fused in mosasaurs (Russell, 1967) and *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 10, 11), these two elements are discussed here as though they were a single fused structure (the elements are not distinguishable in *Pontosaurus lesinensis* [see Pierce & Caldwell, 2004]).

The vomeropalatines of MSNM V3662 are elongate, strap-like elements that parallel the sagittal plane but do not appear to meet at the midline (Fig. 4 A-B). The posterior extent of the bone appears to be beneath the frontal (the palatine ramus), but there is some uncertainty as exposed and this statement must be made only tentatively. Anteriorly, at a point equivalent to the anterior termination of the prefrontal, the vomeropalatine extends a lateral process to contact the maxilla (maxillary process of the palatine); at this point the vomeropalatine continues anteriorly following the margin of the maxillary shelf to the medial divergence of that shelf where it forms the premaxillary process (Fig. 4 A-B). The tips of the vomeropalatine appear to diverge away from the midline as they converge towards the premaxillary process. Details such as the position of Jacobson's Organ, or the aperture of the medial palatine sinus, are not visible as preserved.

Prefrontal

The prefrontal is an anteriorly elongate element with the anterior process extending at least three-fifths of the length of the narial opening along the medial surface of the side wall of the maxilla. Posterodorsally, the prefrontal contacts the frontal along about one quarter of the length of the frontal and then descends ventrally to contact the anterior tip of the jugal and the posterior process of the maxilla. Overall, the exposed surface of the right prefrontal, as preserved, resembles the sail of a tall sailboat (Figs. 2, 3 A-B, 4 A-B). The articulation with the maxilla is an important and characteristic feature of pontosaurs and is shared in common by both species: the suture is long and low and slopes gently towards the narial opening. The result is that there is no ascending process of the maxilla, creating a similar profile to that observed in many extant snakes; this feature contrasts sharply with that described by Caldwell (1999a) for *Coniasaurus gracilodens* where the maxilla has a well-developed ascending process. The difference between *Pontosaurus lesinensis* and *P. kornhuberi* is that in the former the maxilla and prefrontal comprise equal portions of the margin of the narial opening, whereas, as noted for the latter, the prefrontal is three fifths of the margin of the opening.

Nasals

As noted previously, it is not clear from the specimen (Fig. 4 A-B) as to the presence or absence of the nasal bones. This is in direct contrast to the relatively well-preserved nasals of *Pontosaurus lesinensis*, where the nasals are thin, flat and paired, (Pierce & Caldwell, 2004) (Fig. 3 C-D).

Lacrimal

It is not possible to identify the presence or absence of a lacrimal in *Pontosaurus kornhuberi* as the area on either side of the skull, ventral to the prefrontals, is heavily crushed and deformed (Figs. 2, 3 A-B, 4 A-B). As was noted by Pierce & Caldwell (2004), Kornhuber (1873) had reported a trace of the right lacrimal posterodorsal to the maxilla and anterior to the jugal, but such an element was not visible to the former authors. The massive size of the prefrontal would suggest, if analogous to snakes, that the lacrimal is absent in both species of *Pontosaurus* as it is in snakes, *Pachyrhachis* (Lee & Caldwell, 1998) and many other squamate groups (Estes *et al.*, 1988).

Jugal

Both the right and left jugal are well preserved in *Pontosaurus kornhuberi* (Figs. 2, 3 A-B, 5 A-C). The anterior edge of the jugal arch extends forward to meet the prefrontal anteriorly and the maxilla ventrally and may well have extended anteriorly past the orbit as in other mosasauroids (deBraga & Carroll, 1993); this observation is contra the condition reported in *P. lesinensis* by Pierce & Caldwell (2004) except that the anteriormost tip of the jugal is not visible and so may well have overlapped the maxilla, thus extending anterior to the orbit.

A second difference is also noted between the two species: in *P. kornhuberi* the two rami of the jugal form a distinct angle at the posteroventral corner of the orbit producing a well-developed posteroventral tuberosity. In contrast, in *P. lesinensis* the jugal curves gradually in an anterior direction to contact the lateral process of the postorbital. In all other respects, the jugal of *Pontosaurus lesinensis* is of roughly similar size and shape to that of *P. kornhuberi* (Fig. 3 A-D).

Frontal

The frontal is a long, flat element that comprises approximately one-third of the total length of the skull (Figs. 2, 3 A-B, 5 A-B). As is common to pontosaurs and coniasaurs the outline in dorsal view resembles an hourglass that is broadly expanded at both its anterior and posterior ends and is constricted above the orbits (Caldwell, 1999a; Pierce & Caldwell, 2004); this configuration is very similar to that of modern macroteiids (Estes *et al.*, 1988). In *Pontosaurus kornhuberi*, the anterior expansion of the frontal is only marginally more narrow than the posterior expansion at the frontal-parietal suture; this contrasts with the condition in *P. lesinensis* where the anterior expansion is noticeably more narrow than the expansion at the frontal-parietal suture, and with *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 4, 5) where the posterior expansion is twice the width of the anterior expansion.

In *Pontosaurus kornhuberi*, the anterior border of the frontal has only three processes (Figs. 2, 3 A-B, 4 A-B): one large sagittal process and two equal-sized large lateral processes. In contrast, the frontal of *P. lesinensis* has five processes: one large sagittal process, two large lateral processes, and two small parasagittal processes (Fig. 3 C-

D). In both species, the external edge of the lateral processes articulates with the prefrontals, while the internal rim forms the posterior margin of the external narial opening. Pierce & Caldwell (2004) noted that the nasals of *P. lesinensis* were clasped by the unpaired sagittal, and paired parasagittal, processes. The absence of the paired parasagittal processes in *P. kornhuberi* may well relate to the absence of identifiable nasal bones. The sagittal process of *Pontosaurus kornhuberi* is smooth as it is in *P. lesinensis*; in contrast, the sagittal process of *Coniasaurus gracilodens* bears a low but clearly defined sagittal crest that extends posteriorly about one quarter of the length of the frontal.

At its midpoint, the constricted frontal forms the dorsal margin of the orbit. The prefrontal and postorbitofrontal do not meet above the orbits as they do in higher mosasauroids (Russell, 1967), but are widely separated over the orbit as they are in *Pontosaurus lesinensis* (Fig. 3 C-D) and *Coniasaurus gracilodens* (Caldwell, 1999a, figs. 4, 5).

The posterior border of the frontal describes an obtusely angled w-shape along its margin with the parietal; this margin represents a gap of considerable size and is not interpreted as an artifact of preservation, but rather is very well preserved. It is possible that this morphology represents the adult condition and that there was a high degree of mesokinesis in pontosaurs. It is also possible that frontal-parietal ossification was delayed in this animal, either that it was a younger individual or that in fact dermatocranial ossification was delayed in *Pontosaur kornhuberi*. In comparison, the frontal-parietal margin in *Pontosaurus lesinensis* is relatively simple and straight with the two bones fitting together very tightly (Fig. 3 C-D).

Parietal

The parietal is a single element composing approximately one-third of the total skull length (Figs. 2, 3 A-B, 5 C, 6 A-D). In general terms, the suture with the frontal is long and describes an obtuse "w"-shaped outline with large parietal lappets lying below the frontal. Along the lateral edge of the frontal-parietal suture, the anterolateral projection of the parietal is broadly overlapped by the postorbitofrontal. Laterally and ventrally, the parietal is broadly expanded to form a long and deep decensus parietalis (Figs. 3 A-B, 5 C, 6 A) which rises slightly at its midpoint at the sutural contact with an element identified here as the prootic. The dorsal surface of the parietal is not developed into a long thin crest as in *P. lesinensis* (Fig. 3 C-D), but rather is broad, flat table-like surface. The parietal foramen is not as large as that of *P. lesinensis;* it is also an equivalent distance posterior to the parietal-frontal suture in both species.

The prootic margin of the parietal also appears to contact the margin of the supraoccipital; the latter margin is broad and wide in its contact with the parietal and is in the same plane; the supraoccipital does not lie beneath the parietal as in lizards but is in the same plane and articulates along its anterior margin as in snakes. There is also an interdigitating and overlapping sutural contact between the supraoccipital and parietal where the supraoccipital overlies the parietal on the midline in large triangular shaped depression (Fig. 6 A-D). This same condition is observed in *Pontosaurus lesinensis* (Fig. 3 C-D). The differences between *P. kornhuberi* and *P. lesinensis* are preservational: in the former, the overlapping portion of the supraoccipital is broken away leaving a fractured surface on the supraoccipital, whereas in *P. lesinensis* the small sagittal-crest like structure of the supraoccipital is still in place.

The parietal ramus for the suspensorium is well developed though only well preserved on the left side of the skull, where it contacts a small supratemporal element and the small, underlying paroccipital process of the exoccipital-opisthotic. The parietal ramus of *Pontosaurus kornhuberi* is broken away and displaced vertically from its position at the posterior edge of the decensus parietalis. In its proper articulation, the parietal ramus would have been oriented obliquely and would have formed a continuous surface with the decensus parietalis as in *P. lesinensis* (Fig. 3 C-D).

Postorbitofrontal

The postfrontal and postorbital of *Pontosaurus kornhuberi* appear to have fused to form a single, multi-rami element, the postorbitofrontal; the element is very well preserved on the left side of the skull, but very poorly preserved on the right. All descriptions given here are of the left side of the skull. Close inspection indicates the presence of an unidentified element immediately anterior to the left postorbitofrontal (Figs. 3 A-B, 5 A-C) that is considered here to be the left postfrontal. Squamates show a perplexing and problematic degree of plasticity in the presence, absence, or fusion, of the elements comprising the anterior portions of the supratemporal arcade. For example, some groups possess only a postorbital (snakes), while others possess both postfrontals and postorbitals (e.g., *Pontosaurus lesinensis* [Fig. 3 C-D]), while others, such as species assigned to the varanid genus, *Varanus*, and *P. kornhuberi*, possess a single, apparently fused, postorbitofrontal element. Some possess supernumerary elements, such as pythons, which have added a supraorbital bone. Assuming that the anterior element is not a true postfrontal, the remaining description will focus on the morphology of the left postorbitofrontal.

The left postorbitofrontal is a quadri-radiate element with four distinct rami contacting four very different components of the dermatocranium. The anterior or frontal ramus is a moderately long and thin spline of bone that begins at roughly the frontal-parietal suture and clasps the lateral margin of the frontal to a position roughly near the beginning of the supraorbital constriction (Figs. 2, 3 A-B, 5 A-C). The medial or parietal ramus of the postorbitofrontal is very short and medially directed. It clasps the margin of the parietal table just posterior to the frontal-parietal suture; there is a short section of the postorbitofrontal, between the frontal and parietal rami, that firmly abuts the lateral wing of the parietal immediately posterior to the frontal-parietal suture. The lateral or jugal ramus of the postorbitofrontal projects laterally only a short distance; this ramus is thickened posteriorly with
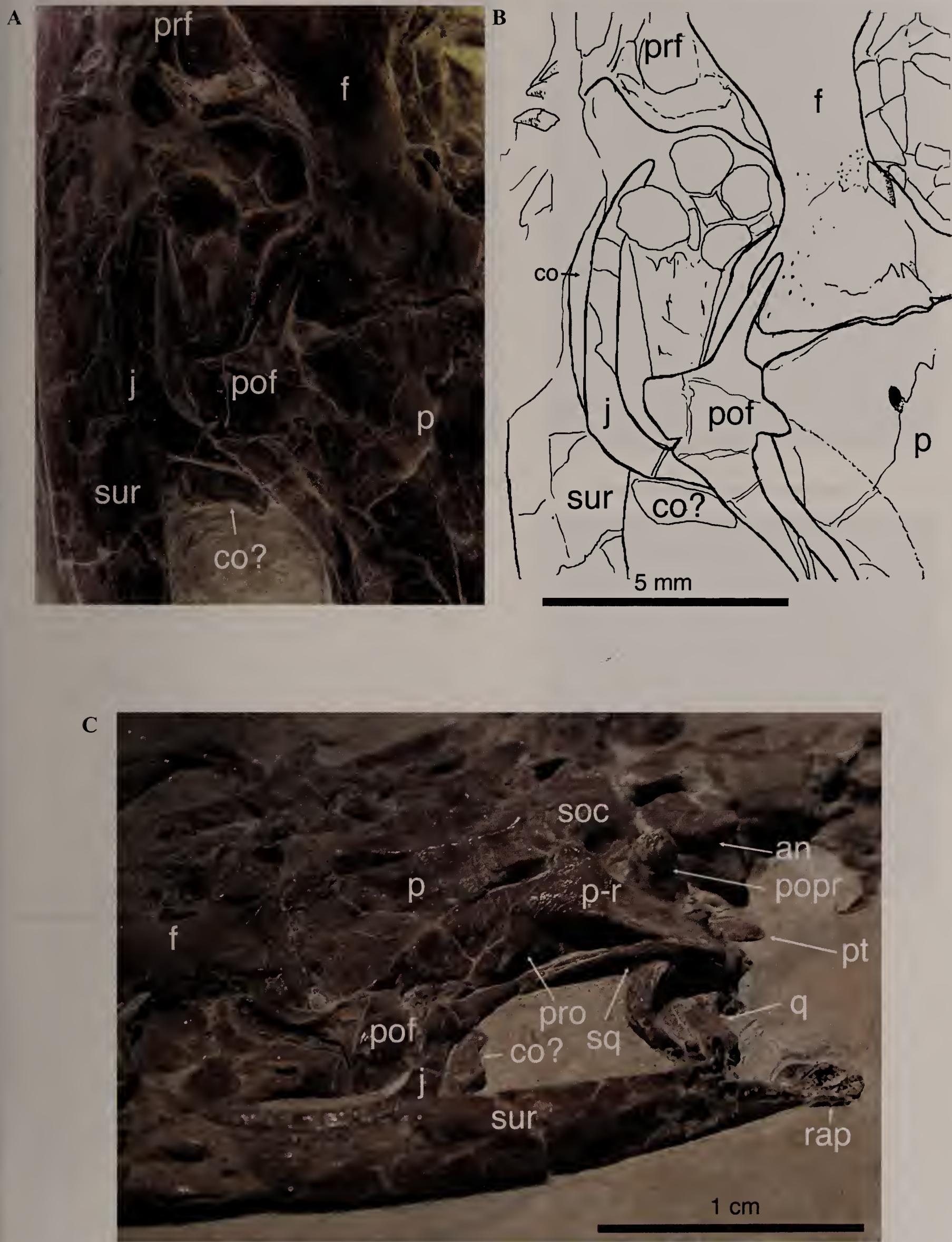
Fig. 5 - Mid-dorsal surface of the dermatocranium of *Pontosaurus kornhuberi*, MSNM V3662. A) Photo detail of left postorbital-frontal-parietal; B) line drawing of same; C) oblique view of left side of skull showing configuration of decensus parietalis and contact with left prootic. Abbreviations: see Fig. 3.
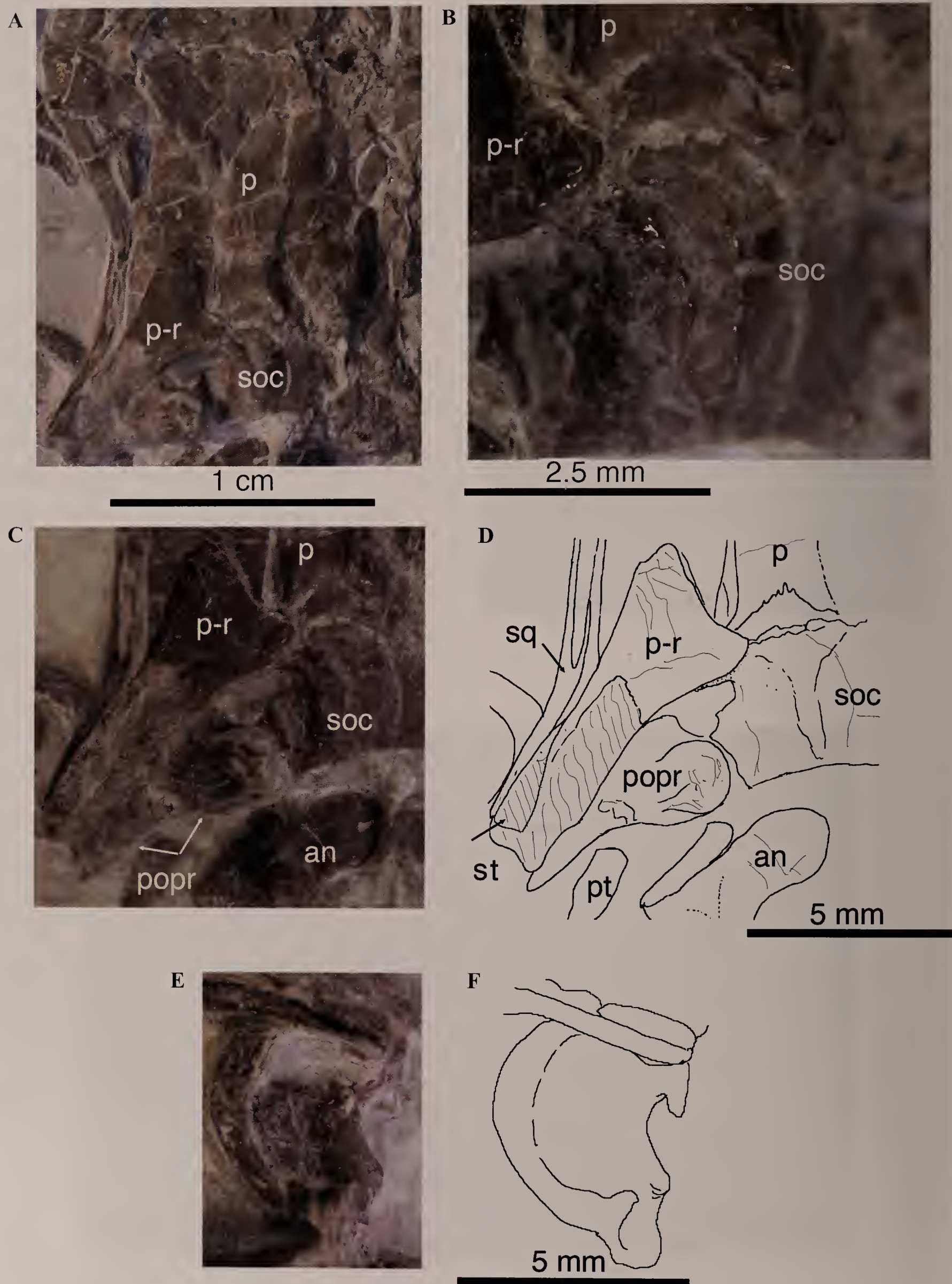
Fig. 6 - Posterodorsal surface of dermatocranium of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of parietal; B) detail of supraoccipital and overlapping, interdigitating sutural contact onto parietal; C) detail of parietal ramus, squamosal, exoccipital, supraoccipital; D) line drawing of 'C'. E) left quadrate. F) line drawing of same. Abbreviations: see Fig. 3.

its anteriormost edge beginning parallel to the plane of the frontal-parietal suture. It is not clear if some portion of the jugal ramus was directed ventrally; however, it is possible that the ascending portion of the jugal contacted a small facet on the ventral surface of the jugal ramus similar to some mosasaurs (Russell, 1967) and many squamates (Estes *et al.*, 1988). The posterior or squamosal ramus of the postorbitofrontal is elongate and thin (Figs. 5 A-C, 6 A-C) extending posteriorly to a point equal to the contact of the parietal and supraoccipital. It overlaps the squamosal laterally and dorsally in an interfingering suture. The distance between the postorbitofrontal bar and the parietal crest is rather far even though the supratemporal fenestra appears to be relatively small anteriorly (Figs. 5 A-C, 6 A-C).

Postfrontal?

It is not clear if the postfrontal is present as a separate element in *Pontosaurus kornhuberi* even though it is clearly separate in *P. lesinensis* (Fig. 3 C-D). The postorbitofrontal, described previously, shows the typical squamate morphology of a fused postorbital ramus and body (posterior ramus contacting the squamosal and framing the supratemporal fenestra, main body contacting the jugal) and postfrontal ramus (anterior process clasping the frontal-parietal suture and extending anterolaterally along the frontal). However, there is an extra element in *P. kornhuberi* that lies anterior and lateral to the anterior ramus of postorbitofrontal the identity of which is uncertain (Figs. 2, 3 A-B, 5 A-C). The element is indicated with a "?" on Fig. 3 B. It is possible that it is a fragment of the pterygoid, or perhaps is a displaced palpebral bone, but as most of the skull is very well articulated, the latter possibility is considered remote. The element bears a striking resemblance to, and is in a similar position to, the postfrontal of *P. lesinensis* which is a large boomerang-shaped element (Fig. 3 C-D) that clasps both the frontal and parietal along its medial border and attaches to, but does not fuse with, the postorbital along its posterolateral surface.

The fusion of the postfrontal and postorbital in forming the postorbitofrontal is not a well-understood process, nor is it common among squamates. It is also clear from a survey of modern squamates that there is great deal of plasticity in the formation and fusion of the dermatocranial elements of the supratemporal and postorbital arcades (see Estes *et al.,* 1988). Non-scolecophidian snakes are considered to possess only a postorbital with the exception of *Dinilysia patagonica* which also possesses a discrete postfrontal (Caldwell & Albino, 2002); amphisbaenians and dibamids possess neither element; *Varanus* possesses a single postorbitofrontal element while *Lanthanotus* and *Heloderma* have only a postfrontal with the postorbital having been lost; anguids typically have both a postfrontal and postorbital, as do most other scincomorphs; gekkotans are treated as possessing a postorbitofrontal even though the posterior ramus is missing and iguanians show both a single element and paired element condition.

Squamosal

The squamosal is a thin band of bone that forms the posterolateral border of the supratemporal fenestra (Figs. 3 A-B, 5 C, 6 C-D). At the midpoint of the supratemporal fenestra, the squamosal articulates with the ramus of the postorbitofrontal; it underlies that element in a long, clasping articulation (Fig. 6 C-D). At its posterior tip, the squamosal contacts the quadrate laterally and the supratemporal medially. The element is slightly bent laterally at its posterior contact with the supratemporal and quadrate. A similar morphology is observed in *Pontosaurus lesinensis* (Fig. 3 C-D).

Supratemporal

The supratemporal is a small wedge of bone that as preserved, appears to articulate with the squamosal, quadrate and parietal ramus. Presumably it also contacted the paroccipital process of exoccipital-opisthotic; however, this is not clear as preserved and it is important to note that the paroccipital process appears to be quite short.

Supraoccipital

The supraoccipital of *Pontosaurus kornhuberi* (Figs. 2, 3 A-B, 6 A-D) is nearly identical in its morphology to that of *P. lesinensis* (Fig. 3 C-D) as reported by Pierce & Caldwell (2004); among squamates the pontosaur supraoccipital is a uniquely configured bone. The element broadly contacts the posterior margin of the parietal along its dorsal surface, not ventrally as in most lizard squamate groups. The element is broadly expanded along this contact and is posteriorly also very broad. The posterior margin of the supraoccipital is rounded and smooth and not emarginated as it is in many lizard squamates. There is no evidence that exoccipital-opisthotic bones met at the midline above the foramen magnum; it appears therefore that the dorsal border of the foramen magnum was formed exclusively by the supraoccipital.

Posterolaterally, the supraoccipital contacts the dorsal margin of the exoccipital-opisthotic bone close to the origin of the paroccipital process. Anterolaterally the supraoccipital appears to contact the posterolateral margin of the decensus parietalis to its contact with the prootic, where the supraoccipital appears to contact that margin in a smooth arc (Fig. 6 A-B).

On median dorsal surface of the supraoccipital (Fig. 6 A-B) is a small t-shaped area of roughened periosteum. On first observation this area appears to be a broken surface, but under high magnification it is clear that a small fragment of unossified tissue likely occupied this region and overlapped the parietal on the dorsal surface of that bone. As the supraoccipital is an endochondral element of the chondrocranium, it is not unlikely that the missing tissue was not ossified. Reconstructing the t-shaped portion and the portion that overlaps the parietal presents a final morphology to the supraoccipital of *Pontosaurus kornhuberi* that is identical to that of *P. lesinensis.*

In *Pontosaurus lesinensis* (Fig. 3 C-D) the supraoccipital has a rectangular base and a clover-shaped anteromedial shelf (Fig. 2). The "stem" and the two lateral "leaves" of the shelf rest on top of, and form a v-shaped suture with,

the parietal; this configuration comes close to that of snakes, but the supraoccipital in snakes never sits above the parietal. Instead the supraoccipital in snakes is level with and slightly on-lapped by the parietal. The third medial "leaf" forms a crest that runs down the center of the supraoccipital's rectangular base. The rectangular base gradually slopes caudally underneath the parietal until it contacts the atlas posteriorly, a configuration that typifies non-snake squamates (Estes *et al.*, 1988). On its lateral margin the supraoccipital meets the left and right exoccipital in a straight, anterior-posterior directed suture.

Exoccipital

As preserved and exposed the exoccipital-opisthotic is a long, curving acute triangle-shaped element with a short, robust paroccipital process. It contacts the supraoccipital dorsomedially, and the prootic anterolaterally. In *Pontosaurus lesinensis* the exoccipital-opisthotic shows exactly the same acute triangle outline, is broad along its contact with the supraoccipital (Fig. 3 C-D), and bears a large, oval paroccipital process ventrally (this process is derived from the opisthotic portion of the exoccipital bone). In *P. lesinensis* the contact with the prootic is not visible while it is visible, though obscured by crushing, on the right side of the skull in *P. kornhuberi* (Fig. 3 A-B).

Prootic?

The right and left prootics are tentatively identified here though it is possible that the fragments identified as prootics are symmetrically fractured portions of the decensus parietalis (Figs. 3 A-B, 5 C). The observable portions of both the right and left prootics are the anterolateral alar processes of the prootic. Ventral to this expansion is an opening or emargination of varying size and shape that serves as the exit point for the Vth and VIth cranial nerves. In lizards such as *Varanus*, the anterior alar process of the prootic contacts the parietal on only a small point at the top of the projection. In snakes, the contact with the decensus parietalis is along the full length of the superior margin of the alar process creating distinct exit points, as foramina for the Vth and VIth cranial. As preserved in MSNM V3662, the type and only specimen of *Pontosaurus kornhuberi*, the decensus parietalis and superior margin of the prootic and alar process also appear to have a continuous sutural contact, unlike the condition in *Varanus*.

Quadrate

The left quadrate is almost perfectly preserved in lateral view in *Pontosaurus kornhuberi* (Figs. 2, 3 A-B, 5 C). It is a C-shaped structure with a pronounced suprastapedial process, a well-developed stapedial notch, a very small but present infrastapedial process, and a well-developed tympanic ala or conch, comparable in particular to that of *Pontosaurus lesinensis*, and more generally, to those of other mosasauroids (Russell, 1967; Carroll & deBraga, 1992; deBraga & Carroll, 1993). As was noted by Pierce & Caldwell (2004), the quadrate of the teiid *Dracaena* (FMNH 207657) is strikingly similar as well. As with *Pontosaurus lesinensis*, the quadrate appears to articulate with the parietal ramus, the squamosal and supratemporal (the latter bone is poorly preserved).

Pterygoid

The pterygoids are not well exposed in MSNM V3662 with only a short section, likely the suborbital portion of the left pterygoid, exposed in the floor of the left orbital opening (Figs. 2, 3 A-B, 5 A-C). Little detail is visible that merits description or comparison to either *Pontosaurus lesinensis* or *Coniasaurus*.

Epipterygoid

Right and left elements that might be identifiable as the epipterygoid are visible on either side of the parietal, between the anteroventral margin of the decensus parietalis and the postorbitofrontal (Fig. 3 A-B). The element is small and rounded in cross-section and directed anteriorly from its contact with the decensus parietalis; this latter position is a taphonomic artifact. While the elements cannot be identified with certainty, they are in the approximate topological position where disarticulated epipterygoids might be anticipated.

A similar element is well preserved in the type of *Pontosaurus lesinensis* (Fig. 3 C-D). The element is a simple, broad, columnar bone whose dorsal tip has taphonomically rotated out of position and is now contacting the postorbital bone directly in front of the postorbital-squamosal suture.

Dentary

The right dentary is not exposed in MSNM V3662, while the left is very poorly preserved and somewhat fractured and fragmented. The left element makes up about two fifths of the length of the mandible (Figs. 2, 3 A-B) and bears at least four mandibular foramina. It is an elongate and very thin element with a large number of teeth; while it is not possible to count the number of tooth positions, it is clear that there is space for approximately twenty teeth. The exposed dentary teeth, like those of the maxilla and those of *Pontosaurus lesinensis,* are laterally compressed, sharp, and weakly recurved with what appear to be shallow furrows or facets. Neither the intermandibular symphysis, nor the intramandibular joint are visible in MSNM V3662 though it seems unlikely that the anatomy of these important joints would have been dissimilar to *P. lesinensis* (Pierce & Caldwell, 2004) or *Coniasaurus gracilodens* (Caldwell, 1999a) and *C. crassidens* (Caldwell & Cooper, 1999).

Coronoid?

An element tentatively identified as part of the left coronoid is present just posterior to the left jugal. The bone fragment as exposed is poorly preserved and it is not clear if it connects to the probable coronoid as exposed beneath the left jugal (Fig. 5 A-C). However, if it is the posterior and dorsal portion of the coronoid, then the dorsal process was quite tall. In comparison, the coronoid process of *Pontosaurus lesinensis* is quite small (Pierce & Caldwell, 2004).

Surangular

The surangular is an extremely long bone who's sutural contacts with the articular/prearticular and angular cannot be ascertained as preserved and prepared. The probable sutural contact with the articular, which would normally be exposed on the posterolateral aspect of the mandible, is broken away just ventral to the articular cotyle and the quadrate (Fig. 5 C); it does appear though that the surangular forms part of the articular surface of the cotyle similar to other mosasauroids. The angular does not appear to be exposed in lateral view. Likewise, no portion of the splenial appears to be visible laterally. The intramandibular joint is also not exposed laterally; unfortunately, at the point were the dentary and surangular meet (Figs. 2, 3 A-C), the bone is broken away and the lateral surface morphology of the joint is obscured. Thus it is not possible to ascertain the presence or absence of the splenial, angular and their contribution to the morphology of the unique mosasauroid and serpentiform joint. The only sutural contact that is relatively well preserved is the surangular-coronoid contact (Fig. 5 A-B); this joint is long and sloping as it rises anteriorly towards the dorsally inflected tip of the jugal. The size and shape of this element is identical to that of *Pontosaurus lesinensis* (Pierce & Caldwell, 2004).

Articular/Prearticular

Details of the sutural relationships between these elements are not visible in MSNM V3662 and so similarities to the fused elements of *Pontosaurus lesinensis* cannot be identified and confirmed. Posteriorly, the articular widens and forms the articular cotyle for the reception of the quadrate. It terminates in an expanded retroarticular process that is well preserved on both sides of the skull.

Postcranial skeleton

The postcranial skeleton of *Pontosaurus kornhuberi* is the most complete of any of the known small aquatic squamates (Fig. 1). Though there is some minor surface breakage and crushing throughout, the postcranium of MSNM V3662 is very well preserved down to the last caudal vertebrae and the tip of the tail (i.e., it is carbonized but present). The cervical vertebrae and ribs are preserved in dorsal view as are the dorsal vertebrae and ribs, and the sacral vertebrae and sacral processes (Figs. 7, 8). Posterior to the sacrum and sacral vertebrae, there appear to be only two pygal vertebrae (based on the absence of haemal arches). Posterior to the pygal vertebrae the axial skeleton is rotated laterally so that the tail and its caudal vertebrae are exposed in left lateral view all the way to the tip of the tail.

In general, the forelimb and girdles are much smaller as compared to the rearlimb and girdles. While the condition in *Pontosaurus lesinensis* is unknown due to the absence of the rearlimb, this marked difference in size between the forelimb and rearlimb is common to *Adriosaurus suessi* (Lee & Caldwell, 2000), *Dolichosaurus longicollis* (Caldwell, 2000) and *Aphanizocnemus libanensis* (Dal Sasso & Pinna, 1997). It is the reverse condition to that of mosasaurs where the forelimb and girdle are much larger than the rearlimb and girdle (Russell, 1967). The condition observed in adriosaurs, pontosaurs, and dolichosaurs also contrasts with nearly identical front and rearlimb proportions in aigialosaurs (Caldwell *et al.*, 1995).

The left pectoral girdle is well preserved and has been slightly translocated so that it is exposed in dorsal view (internal surfaces are exposed); the right pectoral girdle is not visible in any way that permits observation of the elements. Likewise, the left forelimb is much better preserved and is extended lateral to the body wall exposing the elements of the carpus; the right limb is but up and under the body wall with only the distal portion of the manus exposed along the rib cage.

The pelvic girdle is well preserved on the left side of the body but is underneath the sacrum on the right side and is not visible. However, in contrast to the forelimbs, both the left and right rearlimbs are well preserved and exposed in the prepared specimen. The tip of the right femur is hidden beneath the sacrum, where as the entire femur is well exposed on the left side. The tarsus and metapodium and phalanges are all well preserved and exposed.

Axial skeleton

Cervicals

There are ten preserved cervicals in *Pontosaurus kornhuberi*, beginning with C1, represented by the right and left atlas neural arches, and ending with an anterior fragment of C10, identified as such because there is no evidence of an elongate rib articulating with the sternal cartilages (Figs. 7 A-D, 8 A, 9). The cervical series are all preserved in dorsal view, and for the most part have been sheared through the neural arch lamina leaving only the centrum and fragments of the neural canal; one vertebra, C8, was prepared from the right lateral side to expose the cervical peduncle and unfused hypapophysis.

The cervical vertebrae gradually increase in width and length caudally (Fig. 7 A-C). The right and left neural arches along with the anterior portion of the axis centrum are visible in dorsal view (Fig. 7 A-D). Pre- and postzygapophyses are variably present, depending on preservation, from C3-C10. Synapophyses/parapophyses are present from C3-C10; C1 and C2 do not appear to possess cervical ribs, a condition typical of squamates. Short cervical ribs are preserved from C3 to C7 on the left side, and on C4, C6 and C8 on the right side. It is not clear, due to preservation, if any of the vertebrae possesses zygosphenes or zygantra.

For *Pontosaurus lesinensis* Kornhuber (1873) had originally identified a total of nine cervicals, but what he thought was the atlas-axis complex is actually C3 (see Pierce & Caldwell, 2004). Furthermore, based on morphology and the position of the pectoral girdle, what Kornhuber identified as the first two dorsals corresponds to the last two cervicals. Therefore, by making the appropriate changes, the cervical count increases to twelve. In
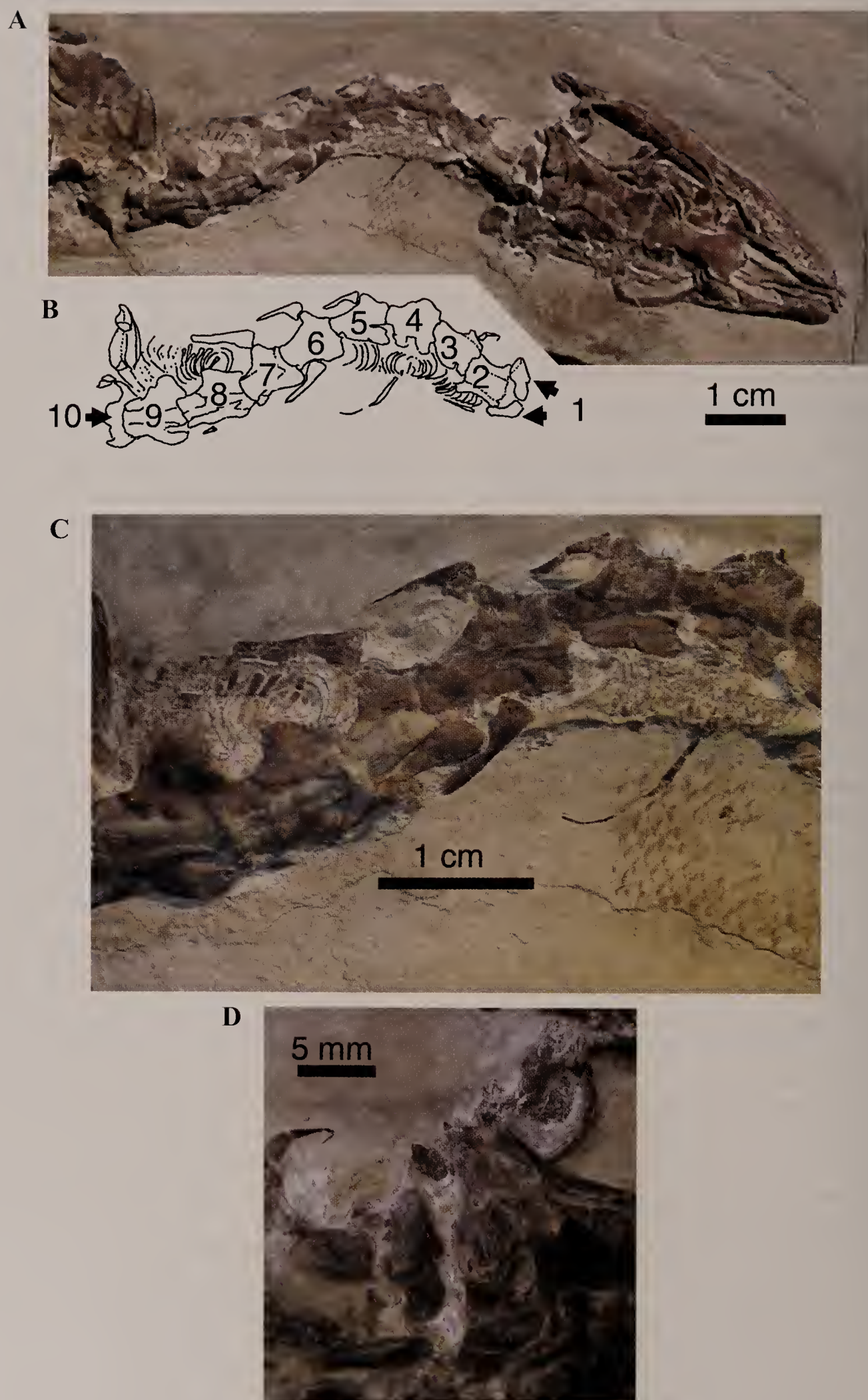
Fig. 7 - Cervical vertebrae of *Pontosaurus kornhuberi*, MSNM V3662. A) Photographic overview of entire cervical column; B) line drawing of only the cervical column (numbers indicate 1-10 cervical vertebrae); C) detail of mid and posterior vertebrae in cervical column showing cervical ribs, neck scales, and tracheal rings; D) detail of C1 (note right and left atlas neural arches are flattened and compressed).

squamates, a cervical count greater than ten has only ever been observed in pachyophiids (Lee & Caldwell, 1998; Lee *et al.*, 1999), pontosaurs and dolichosaurs (Dal Sasso & Pinna, 1997; Caldwell, 2000; Lee & Caldwell, 2000; Pierce & Caldwell, 2004).

Dorsals

There are twenty-six dorsal vertebrae present in MSNM V3662 (Figs. 1, 8 A-B, 10 A). The first and last three dorsal vertebrae in the series are poorly preserved but the ribs associated with the left synapophyses are present and quite well preserved making the count of dorsals quite accurate. In general, the vertebrae and ribs increase in size and in degree of pachyostosis from the first dorsal to approximately the twenty-first to twenty-second vertebra; at this point there is a marked reduction in the degree of pachyostosis and overall size of both the ribs and vertebrae (Figs. 8 A-B, 9, 10 A, 11 A). The 23rd-26th ribs decrease in size and thickness posteriorly and extend laterally from the centra in a narrow downward arch folding towards the mid-line and forming a somewhat laterally constricted frame; these last three ribs do not show any notable degree of pachyostosis (Fig. 11 A). In *Pontosaurus lesinensis* a corresponding decrease in pachyostosis begins at dorsal vertebra 21.

Pre- and post-zygaphophyses are present, but for the most part poorly preserved. In the few vertebrae with preserved zygapophyses, the facets do not appear to incline above the horizontal; however, it must be remembered that there is considerable compression of the specimen in addition to the fracturing present on most vertebrae. Accessory articulations, specifically zygosphene-zygantral facets are present in the dorsal column but can only be observed in the mid-dorsal region on vertebrae fifteen through twenty.

For *Pontosaurus lesinensis*, Kornhuber (1873) originally counted 30 dorsals, but with the modified count in the cervical region given by Pierce & Caldwell (2004), the dorsal count is now recognized to be 28, for a total of 40 presacral vertebrae. For *P. kornhuberi* the count is similar: 10-11 cervicals plus 26-27 dorsals for a total of 36-38 presacrals. The dorsal vertebrae of both species are larger than the cervicals in width and length and are more robustly ossified (Figs. 1 A-B, 7 A-D, 8).

Sacrals

In *Pontosaurus kornhuberi* the left pelvic region is very well preserved, but the sacral vertebrae are missing completely even though fragments of the first sacral transverse process and a complete second sacral transverse process are present (Figs. 8 A, 11 A-B). Based on the articulations of the first and second transverse processes, there are clearly only two sacral vertebrae, a feature common to most squamates with a sacrum. The transverse process of the first sacral vertebra is largely broken away where it would have overlain the ischium; however, there are some remnants of the proximal portions of the process between the ischium and the vertebra. The second sacral vertebra's transverse process is missing as well, but an excellent natural mold of the ventral surface of the process is preserved; the distal tip of the mold still retains some fragments of bone such that the articulation with the ilium is preserved. A third vertebra and transverse process is located next to the ilium (Fig. 11 A-B) but is not fused to it and is interpreted here as the first pygal vertebra. In *Pontosaurus lesinensis* the specimen is broken through the sacrum preserving very few details of the anatomy of this region. Pierce & Caldwell (2004) reported the presence of two fragmentary transverse processes that they interpreted as belonging to sacral vertebrae.

Pygals?

There appear to be only two pygals, contra Dal Sasso & Renesto (1999) who identified three, in *Pontosaurus kornhuberi* (Figs. 8 A, 11 A-C) based on the absence of haemal arches; pygal vertebrae in pythonomorphs are differentiated from caudals based on the absence of haemals. However, it is important to point out that the ventral surfaces of these two most postsacral vertebrae are not observable and thus haemapophyses and their attendant haemals cannot be ruled out completely. The difference in haemal counts between this study and that of Dal Sasso & Renesto (1999) is based on the position of the first preserved haemal between the transverse processes of the third and fourth vertebrae posterior to the sacrum (Figs. 8, 11 C). I tentatively identify these two vertebrae as pygals.

These two probable pygals, like the sacrals and dorsals, are broken through the neural arches and preserve little information on the morphology of the zygapophyses and neural arches. Unlike the caudals, the pygals are not preserved in lateral view and so the left transverse processes are well preserved displaying their dorsal surfaces. The first pygal vertebra's transverse process has an unusual morphology as compared to that of the second pygal (Fig. 11 A-C); the process is anteriorly directed and narrows towards the tip resembling a small "j"-shape. This morphology is not atypical of pygal or first caudal vertebrae as these transverse processes are usually modified to support lymph node clusters located superior to the cloaca; such transverse processes are referred to as lymphapophyses. By comparison, the transverse process of the second pygal is directed laterally, is narrow at the distal tip and widest proximally. The next most posterior vertebra is also preserved in oblique dorsal view but is identified here as the first caudal based on the estimation that its posteroventral margin articulated with the large disarticulated haemal arch located to the left of it (Figs. 8 A, 11C).

Caudals

The tail is extremely well preserved, numbering 163 caudal vertebrae from the last pygal to the tip of the tail; at the tail tip the vertebral count is problematic due to the extremely small size of these most-caudal elements (Fig. 8 A, C-F). Overall, the caudal vertebrae are strongly laterally compressed and longer than they are tall and wide. The tips of the haemals are fused so that they form a true haemal arch, however the arches articulate with the haemapophyses instead of being fused to them. Haemals

are present along the tail to caudal vertebra 139. For approximately the first 55 caudal vertebrae, the haemal arches are nearly twice as long as the neural spines; by about vertebra 55-60, the haemals and neural spines are nearly the same length. From this point, to vertebra 139, where preserved, the haemals and neural spines are of equal length. The anteriormost 60 vertebral elements make up slightly more than half the length of the tail, with the remaining half of the length containing the other one hundred and three vertebrae. The effect on the aspect of the tail is that for at least the first half of its length, the hypaxial depth is nearly twice that of the epaxial depth based on osteology alone; factoring in the soft-tissue effect on tail aspect, it becomes clear that ventral to the haemal arches the tail is at least that same haemal depth again (Fig. 8 C-D). Epaxially, the marginal squamation indicates a soft tissue depth equal to the height of the neural spines. Thus, between its osteology and soft tissue anatomy, the tail of *Pontosaurus kornhuberi* was at least twice as deep as the osteology would suggest.

The first and second caudals possess large transverse processes and are preserved in dorsal view. However, each has a large transverse process, equivalent in length to those of the two pygal vertebrae (Fig. 11 A-C). For all four of these vertebrae it is likely that the varied heads of the *m. caudofemoralis* originated here. This muscle body is integral to strong tail driven propulsion and requires significant origin sites if it is to be a useful locomotory muscle.

All caudal centra are longer than they are tall, which is the opposite condition to that observed in mosasaurids and aigialosaurids (Russell, 1967; deBraga & Carroll, 1993). Another interesting feature is the rather steep posterior angle of all neural spines along the column. This inclination would suggest fairly strong ligamentous connections of the varied *m. spinocaptis* muscles between vertebrae.

The very small vertebrae of the distal tip of the tail are slightly disarticulated and bent backwards on each other so that in a very small area (approximately 1.5 cm) there are thirteen caudal vertebrae. The distal carbonized tip of the tail contains no vertebral centra (Fig. 8 F).

Pectoral girdle and forelimb

The left pectoral girdle is relatively well preserved and exposed in internal view. Fragments of the scapula are preserved, as are portions of the clavicle, interclavicle, coracoid, supracoracoid and sternal cartilage (Figs. 9, 10 A). The right forelimb is not well exposed in *Pontosaurus kornhuberi*, having twisted beneath the body during burial. However, the left forelimb is very well preserved and is exposed in palmar view (Fig. 10 A-E). This description will therefore focus on the left forelimb.

Scapula and coracoid

The scapula and coracoid may well be fused into a single scapulocoracoid element similar to that of the aigialosaur *Opetiosaurus* (Carroll & DeBraga, 1992; DeBraga & Carroll, 1993) and *Pontosaurus lesinensis*, but as preserved, it is not absolutely clear; the alternative, as in most aigialosaurs (Carroll & DeBraga, 1992) and both *Coniasaurus gracilodens* (Caldwell, 1999) and *Dolichosaurus longicollis* (Caldwell, 2000) is that the two elements are separate. Evidence suggesting that there was fusion of these two elements is derived from the absence of an identifiable sutural contact along the anterior margin of the coracoid. Additionally, because the scapula is a small element in *P. kornhuberi* and is not well preserved, it is not clear if it is emarginated (in *P. lesinensis* it is not emarginated). Similar to mosasaurs (Russell, 1967; DeBraga & Carroll, 1993), *Haasia* (Polcyn *et al.*, 1999), *Coniasaurus gracilodens* (Caldwell, 1999) and *Aphanizocnemus* (Dal Sasso & Pinna, 1997), the coracoid portion is significantly larger, possesses an anterior (primary) emargination and a fan-like posterior margin. A single coracoid foramen is present in the middle portion of the element.

Supracoracoid cartilage

The exact outline of the supracoracoid cartilage is not clear as its contact with the sternal cartilage is not well-preserved; the only point where its contact with the sternal cartilage is clear is immediately to the right of the humerus where the supracoracoid cartilage is seen to extend past and overtop of the sternal cartilage (Fig. 9). However, the semi-circular outline of the supracoracoid cartilages contact with the coracoid is well defined, indicating that the coracoid was mobile within the supracoracoid cartilage assembly.

Interclavicle

The interclavicle is represented by the left transverse process lying to the left of C10 and immediately anterior to the element identified as the clavicle (Fig. 9), and by the sagittal ramus extending parallel to the long axis of the body immediately to the right of the supracoracoid cartilage. As exposed, the sagittal ramus of the interclavicle only extends posteriorly to the mid-point of the coracoid; likely, as preserved and prepared, the distal extent of the ramus is incomplete. The interclavicle of *Pontosaurus lesinensis* is similar in shape but slightly longer as preserved (Pierce & Caldwell, 2004).

Clavicle

The clavicle is a relatively robust element that is broken on both its proximal and distal extremities leaving little to describe of its anatomy other than to say it shows a sloping curvature at midlength.

Sternal cartilage

The sternal cartilage is calcified, exposed in internal view, with only the left side of the element exposed in MSNM V3662. There are three posteriorly directed articular points for costal cartilages (Fig. 9). The element is not exposed far enough posteriorly to determine if the third costal articulation point is the last, minus the xiphisternal cartilage articulations, as observed in *Dolichosaurus longicollis* (Caldwell, 2000) which also only has three costal car-
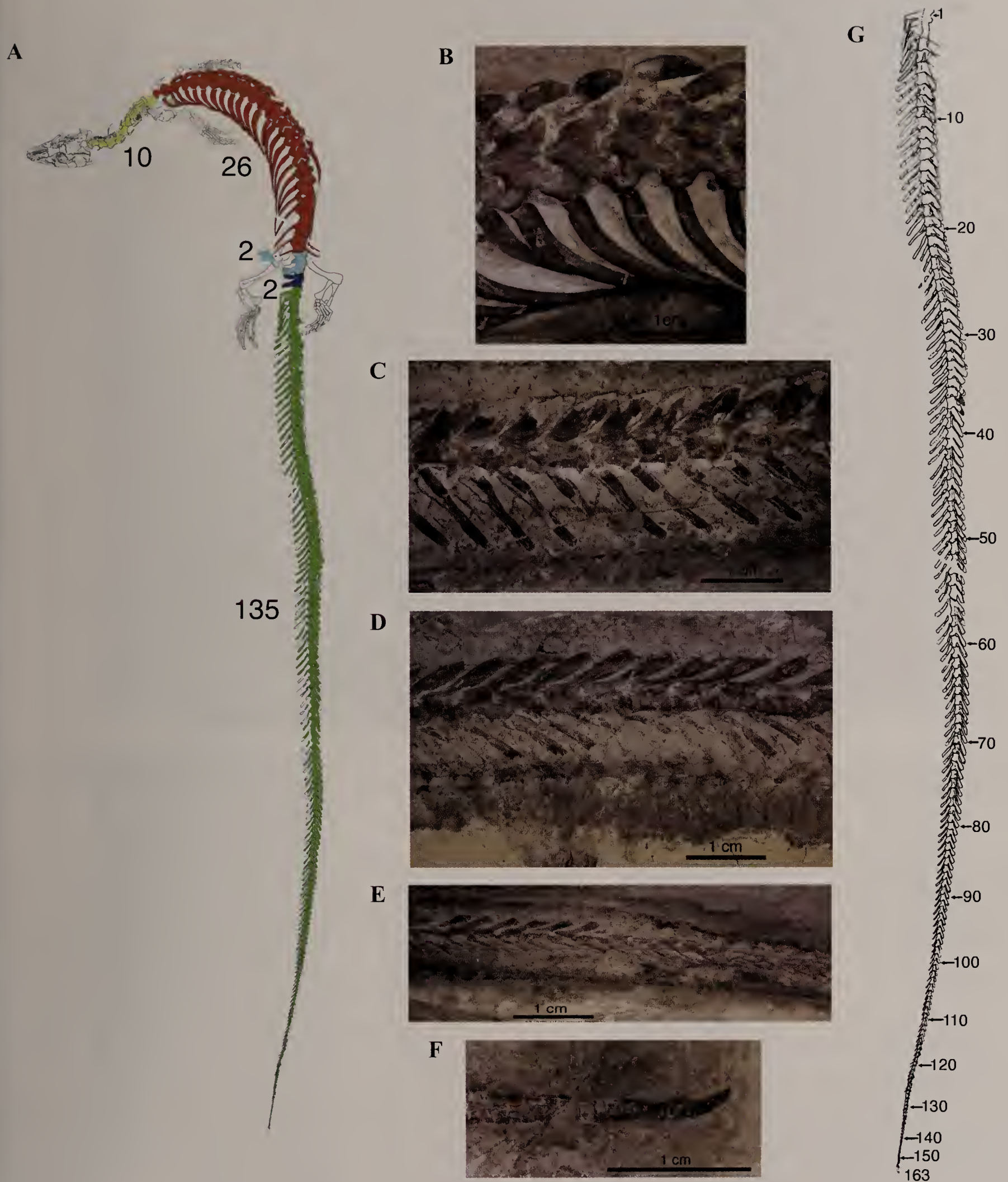
Fig. 8 - Axial skeleton of *Pontosaurus kornhuberi*, MSNM V3662. A) Line drawing of MSNM V3662 with axial skeletal regions colour coded (yellow=cervical; red=dorsal; light blue=sacral; dark blue=pygal; green=caudal); B) detail of dorsal vertebrae and ribs; C) anterior caudals; D) mid-caudal vertebrae; E) distal caudals; F) distal-most caudals to soft-tissue tip of tail; G) line drawing of caudal skeleton indicating numbers of vertebrae along the column (1-163).
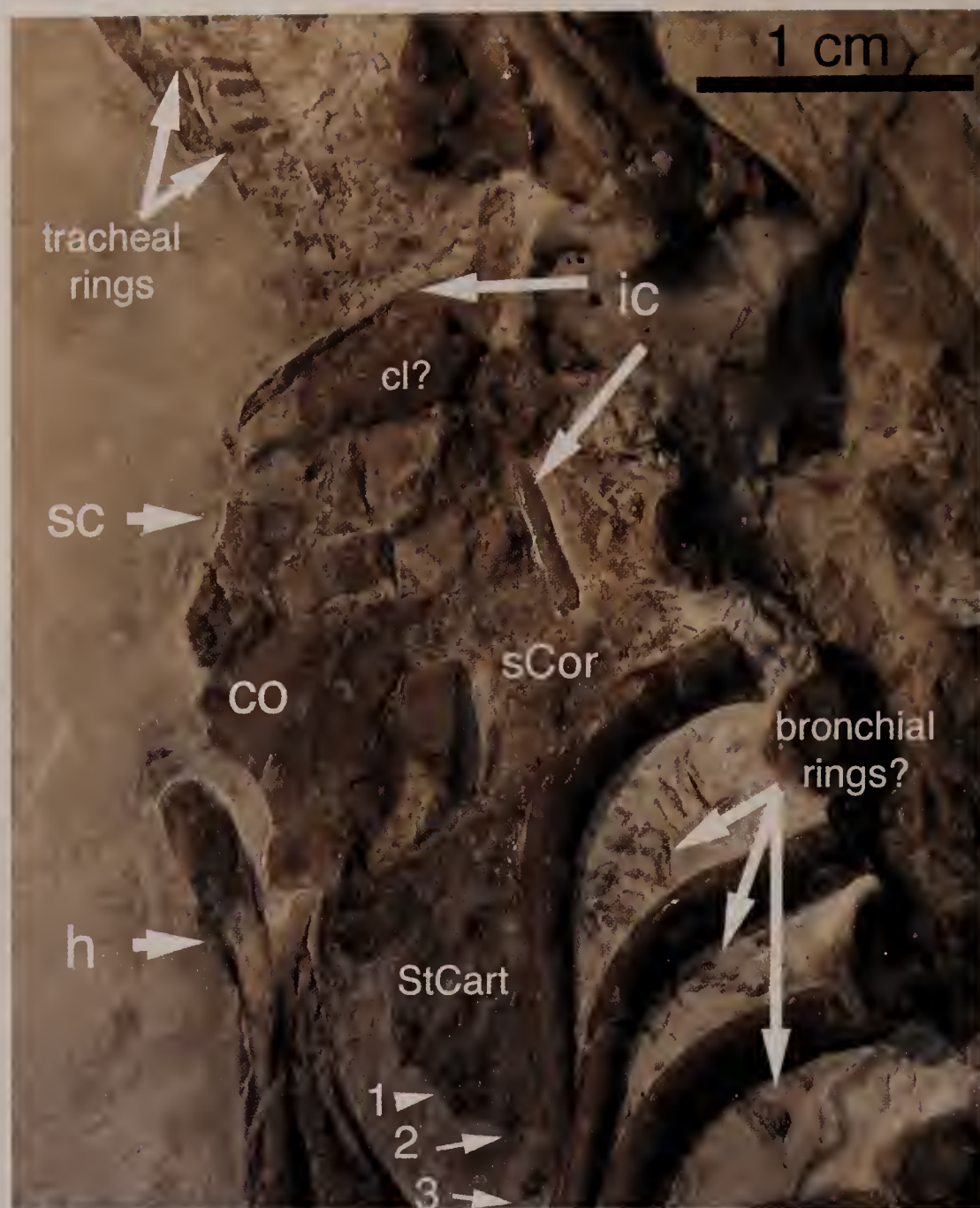
Fig. 9 - Pectoral girdle of *Pontosaurus kornhuberi*, MSNM V3662. Abbreviations: cl?, clavicle; co, coracoid; h, humerus; ic, interclavicle; sc, scapula; sCor, supracoracoid cartilage; stcart, sternal cartilage; 1-3, costal cartilage articulation points.

tilage articulations on the sternal cartilage. The number contrasts with the aigialosaur *Carsosaurus marchesetti* (Caldwell *et al.*, 1995) where there are at least five costal cartilage articulation points in addition to the xiphisternal cartilages.

Humerus

The humerus is a short element (16.5 mm long), crushed throughout most its length, and is slightly constricted at mid-shaft and expanded at both ends. There is no evidence of a proximal epiphysis though the humeral head is slightly broken away medially (Fig. 9). The distal expansion appears to possess a small-ossified epiphysis at the contact with the ulnar head (Fig. 10 A). Both the ectepicondylar and entepicondylar foramina are absent. Proximally, near the broken portion of the head, there is a stout tubercle and small crest for the attachment of the deltoid musculature. Distally, there is a large somewhat flattened capitulum and a troclea; although the dimensions are smaller, the distal epiphysis resembles that of *Opetiosaurus* (deBraga & Carroll, 1993) and *Haasia* (Polcyn *et al.*, 1999).

Radius and ulna

The radius and ulna are of similar size and are distally divergent along their contact with the proximal row of carpals (Fig. 10 A-C); proximally the two elements are in close contact along the distal margin of the humerus. The effect of this divergence is that the antebrachium, and thus forearm, is extremely wide and flattened. It is also likely that pronation of the forearm was not possible thus impeding forelimb assisted terrestrial locomotion. This form of distal divergence is observed in most mosasaurs (Russell, 1967) and the dolichosaurs *Adriosaurus* (Lee & Caldwell, 2000) and *Pontosaurus lesinensis* (Pierce & Caldwell, 2004). Divergent epipodials also characterize aigialosaurs such as *Carsosaurus marchesetti* (Caldwell *et al.*, 1995) and *Opetiosaurus bucchichi* (Carroll & deBraga, 1992) but to a much lesser extent and it appears as though pronation of the manus was possible due to the configuration of the radius.

In *Pontosaurus kornhuberi* the radius is a simple rod-like element that is slightly curved along its antebrachial margin. The ulna is thickened proximally forming a weak olecranon process, is narrow through the antebrachial portion of the shaft, and then expands somewhat at the contact with the ulnare.
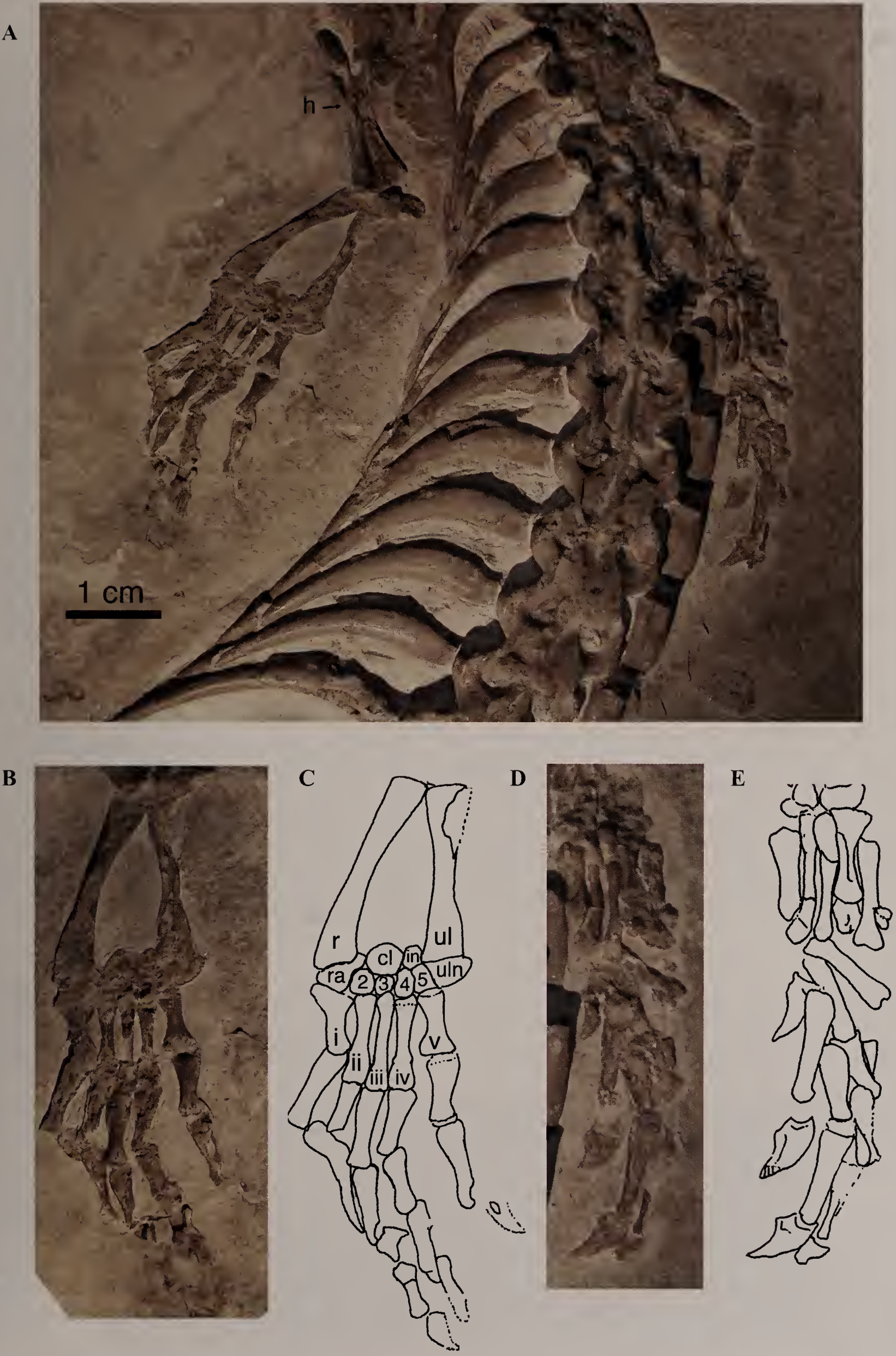
Fig. 10 - Forelimbs of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of anterior trunk and right and left forelimbs; B) photodetail of left forelimb; C) line drawing of left forelimb; D) photodetail of right forelimb; E) line drawing of right forelimb. Abbreviations: cl, centrale; h, humerus; in, intermedium; r, radius; ra, radiale; ul, ulna; uln, ulnare; i-v, metacarpals 1 through 5; 2-5, distal carpals 2 through 5.

In general, the propodial and epipodials are comparable to those of *Pontosaurus lesinensis* (Pierce & Caldwell, 2004) and the dolichosaur *Adriosaurus* (Lee & Caldwell, 2000) in terms of proportions. Comparisons of this sort highlight several interesting trends. Of importance to note in *P. kornhuberi* are the relative proportions of the podial elements: the humerus (propodial) and ulna/radius (epipodials) are of equal length and make up two fifths of the length of the limb, while the hand (mesopodium, metapodium and phalanges) comprises the other three fifths of the limbs overall length. There are three apparent trends in the evolution of the pontosaur limb: 1) overall reduction of the limbs relative to body size; 2) size reduction of the forelimb in relation to the rearlimb; 3) increased size of the manus/pes in relation to the propodials and epipodials.

Mesopodium (carpus)

The mesopodium possesses both a proximal and distal row of carpals (Fig. 10 A-C). The proximal row includes the radiale, medial centrale, and intermedium, while the distal row includes the ulnare and distal carpals two through five. There is no pisiform as preserved and prepared though it is possible that the postaxial tip of the ulnare is the pisiform (the surface of most of the bones of the epipodium and mesopodium is broken away and so sutures are hard to identify).

The radial and ulnare are the largest mesopodial elements in the carpus and are both irregularly shaped, lozenge-like elements. The radiale articulates with both the centrale and distal carpal two; the centrale appears to contact the radiale, distal carpals 2 through 4, as well as the intermedium. The intermedium is a small element displaced postaxially by the large centrale (Fig. 10 B-C). The mid-antebrachial placement of the centrale, and the comparatively small size of the intermedium, is a consistent feature among aigialosaurs (Caldwell *et al.*, 1995; Caldwell, 1996) and now pontosaurs (see Pierce & Caldwell, 2004).

Metapodium

All five metacarpals are present (Fig. 10 A-E). The first and fifth are shorter than two, three and four, and as a result are more hourglass-shaped than the longer and slimmer metacarpals two through four. The fifth metacarpal articulates with distal carpal five but not the ulnare. Likewise, metacarpal one articulates with only the radiale, while the remaining metacarpals articulate with their respective distal carpals.

Phalanges

The phalangeal formula appears to be 2-3-4-5-3, a count that is primitive for all lepidosauromorphs (Fig. 10 A-E). The distal phalanges of digits three, four and five are not well preserved but a count is still possible from the natural molds. The phalanges of all digits are roughly the same shape: proximally expanded, narrow shaft, and distal condyle with two condylar heads. The terminal phalanx or ungual is a well-defined claw with a proximal and ventral tubercle.

Pelvic girdle and rearlimb

The right pelvic girdle is not exposed (Fig. 8 A). However, the left girdle is more complete and reasonably well preserved. The left pubis is well preserved as is the left ischium; the left ilium is preserved throughout most of its posterior length as a natural mold of the ventral portion of the bone within only the acetabular portion preserved as a fragment of bone.

Ilium

The ilium of *Pontosaurus kornhuberi* is slightly expanded at the contact with the ischium and pubis; posterior to the acetabular fossa (not well preserved in its entirety in MSNM 3662) the ilium is posteriorly elongate (i.e., the posterior superior iliac crest), articulates with two sacral processes and overlaps at least one pygal vertebra, possibly two (Fig. 11 A-C). There is no evidence of an anterior superior iliac crest, as the bone appears to terminate at the contact with the pubis in the middle of the acetabular fossa. This same anatomy (posterior iliac crest, no anterior crest) is shared with all aigialosaurs (Caldwell *et al.*, 1995) and *Dolichosaurus longicollis* (Caldwell, 2000) and contrasts with the anteriorly directed superior iliac crest/spine of mosasaurs (Russell, 1967) and the condition in modern terrestrial lizards where both crests are present (though the anterior is smaller, e.g., *Varanus*).

Pubis

The pubis is small as compared to extant terrestrial lizards, but still displays the typical hatchet-shaped morphology; there is a large pubic foramen at the center of the proximal head of the bone (Fig. 11 A-B). Distal to the pubic head, the element narrows to a long medially directed shaft that expands slightly where it contacts the right pubis at the midline. The head of the pubis bears two principal facets: 1) laterally for the head of the femur, 2) medially, for articulation with the ilium. The ischiadic facet is not visible as preserved and prepared.

Ischium

The ischium is slightly shorter than the pubis and has been displaced from its ventral and posterior position (Fig. 11 A-B). The element is curved along its anterior margin and steeply angled along its posterior margin to form an equine-ankle like shape. The proximal portion is narrower than the distal tip (ischiadic footplate), the latter of which articulates with the opposite footplate of the right ischium.

Femur

The femur is a long (33 mm long) and relatively robust bone (Fig. 12 A) that is nearly twice the length of the epipodium (tibia and fibula are each 18 mm in length). As compared to the humerus (16.5 mm long) it is twice the length of that bone, and compared to the ratio of nearly 1:1 between the humerus and radius/ulna, the femoral/tibia-fibula ratio is quite different at roughly 1.8:1.

The proximal tip of the left femur preserves a rounded epiphysis still in articulation with the acetabular fossa (Figs. 11 A-B, 12 A). The proximal portion of the element is rela-
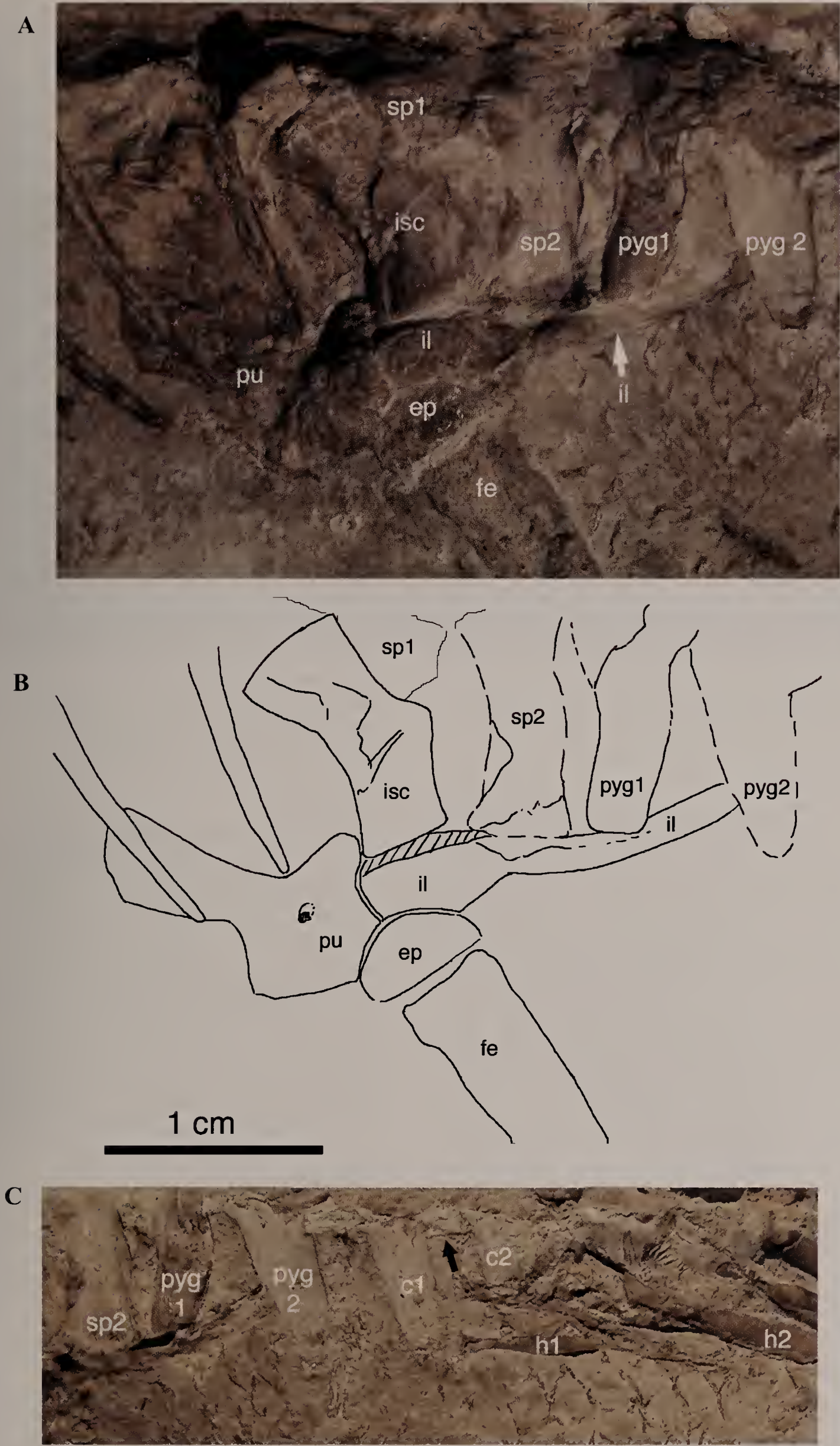
Fig. 11 - Pelvic girdle of *Pontosaurus kornhuberi*, MSNM V3662. A) Photodetail of left pelvis; B) line drawing of same; C) photo detail of pygal region. Abbreviations: c1-2, first and second caudal vertebrae; ep, epiphysis; fe, femur; h1-2, haemal arches; il, ilium; isc, ischium; pu, pubis; pyg 1, 1st pygal vertebra; pyg 2, 2nd pygal vertebra; sp1-2, sacral processes 1 and 2.

tively narrow compared to the expanded distal portion. There are no strongly developed trochanters on the proximal head, nor are there any well developed femoral condyles at the articulation with the tibia and fibula. The only relatively well-developed feature visible on both the right and left femora is a slight anterior curvature of the shaft of the bone. The surface bone of the right femur is better preserved than the left and indicates that the mid-line of the shaft bears a long proximal-distal crest, postaxial to which is an equally long and shallow fossa. It is likely that this portion of the femur served as the insertion point for the *m. caudofemoralis* discussed previously in terms of the pygal and anterior caudal vertebrae and their transverse processes.

Tibia and fibula

The tibia and fibula, like the radius and ulna, are of similar size and are distally divergent along their contact with the proximal tarsal row (Fig. 12 A-C); proximally the two elements are in close contact along the distal margin of the femur. The effect of this distal divergence is that the antebrachium, and thus lower limb, is wide and flat as noted previously for the forelimb (Fig. 10 A-E) and in mosasaurs and other dolichosaurs. In *Pontosaurus kornhuberi* the tibia is a simple rod-like element that is slightly curved along its antebrachial margin and is much more gracile than the fibula. The fibula is much more narrow at its proximal end than the distal end (2:1 ratio) that expands into a large fan-shape distally. The fibula articulates with both the calcaneum and astragalus.

Mesopodium (tarsus)

The tarsus possesses both a proximal and distal row of tarsals (Fig. 12 A-C) and is the best-preserved tarsus of any known member of the Dolichosauridae, *sensu* this study (see also Caldwell, 1999a, 2000; Lee & Caldwell, 2000). The proximal row includes the postaxially located calcaneum, the astragalus, situated in the antebrachial space, and an extra element identified in Fig. 12 B-C with a "?". This extra element is common to both the right and left pes and is in articulation in the left pes where it is located ventral to the tibia and preaxial to the astragalus; in the right pes this element has been disarticulated into the antebrachial space by the distal movement of the tibia (Fig. 12 A-C). The identity of this extra element is problematic. In the left pes it would be easy to dismiss this bone as a tibial epiphysis. However, in the right pes, this is clearly not the case. Instead, the possibility is raised that this preaxial element is a separate center of astragalar cartilage ossification, or, that it is a distal tarsal two that has been displaced.

The morphology of the astragalus is similar to that known for pythonomorphs (see Caldwell, 1996, fig. 15) where the element is not fused to the calcaneum as in modern squamates, but instead is a large element, dominating the proximal tarsal row, bears a "u"-shaped emargination of finished perichondral bone across the distal expanse of the antebrachium, and has a distinct tibial and fibular facet of roughly equal size and articulates with a small, lozenge-shaped to irregularly shaped calcaneum (Fig. 12 A-C).

The distal tarsal row includes only two elements, distal tarsal three and four (Fig. 12 A-C). Distal tarsal four is the larger of the two as preserved in the right pes (Fig. 12 A, C) and articulates preaxially with the smaller distal tarsal three. However, postaxially distal tarsal four also appears to be in contact with a bony mass of uncertain identity (Fig. 12 A-C). In comparison, in the left pes, distal tarsal four is again well preserved, but distal tarsal three is not preserved or is preserved unprepared below the tip of metatarsal three, such that this articulation is not obvious. However, there is a distinct ossification postaxial to distal tarsal four that may be the same element as indicated in the right pes. In mosasaurs the tarsus only ever includes a small calcaneum, large astragalus and distal tarsal four (Caldwell, 1996). In aigialosaurs (Caldwell *et al.*, 1995) the tarsus includes a small calcaneum, large astragalus and distal tarsals three and four. The tarsus of *Pontosaurus kornhuberi* shares the presence of an ossified third tarsal with aigialosaurs to exclusion of this element in mosasaurs.

The additional postaxial element may well be the poorly ossified portion of the hook on the fifth metatarsal or it may represent the actual fifth metatarsal with the element so identified in *Pontosaurus kornhuberi* being the first phalanx (Fig. 12 A-C). If this is the case, then this anatomy would be consistent with that seen in mosasaurids (Caldwell, 1996) where the hooked fifth metatarsal, a usually consistent feature of squamates, is absent, but there the fifth metatarsal is a small, compressed element that articulates distally with a first phalanx that is of subequal size and shape to the other metatarsals.

Metapodium

Five metatarsals are identified with the caveat as identified previously, i.e., that the actual fifth metatarsal might be the element identified with a "?"-mark in Fig. 12 A-C. However, using the identities as illustrated, in the manus, the first and fifth are shorter than two, three and four, and as a result are more hourglass-shaped than the longer and slimmer metatarsals two through four. An important difference is that the fifth is shorter than the first and is much less robust while the first is the thickest and most robust element in the pes. Due to some slight disarticulation and dissociation, the articulations of the metatarsals with the more proximal elements of the tarsus are not clear.

Phalanges

The phalangeal formula appears to be 2-3-4-5-3 thus showing a limited form of phalangeal reduction of the fifth digit by loss of one phalanx (Fig. 12 A-C) unless the argument rendered previously is accurate and the fifth metatarsal is represented by the broken fragments in Fig. 12 A-C. If this is the case, then the phalangeal formula is not derived, but rather is the primitive configuration of 2-3-4-5-4.

The phalanges of the pes are morphologically similar to those of the manus: proximal expansion, narrowed shaft, and distal condyle with two condylar heads. Again, the terminal phalanx or ungual is a well-defined claw with a proximal and ventral tubercle for ligamentous attachment and a sharp tip.
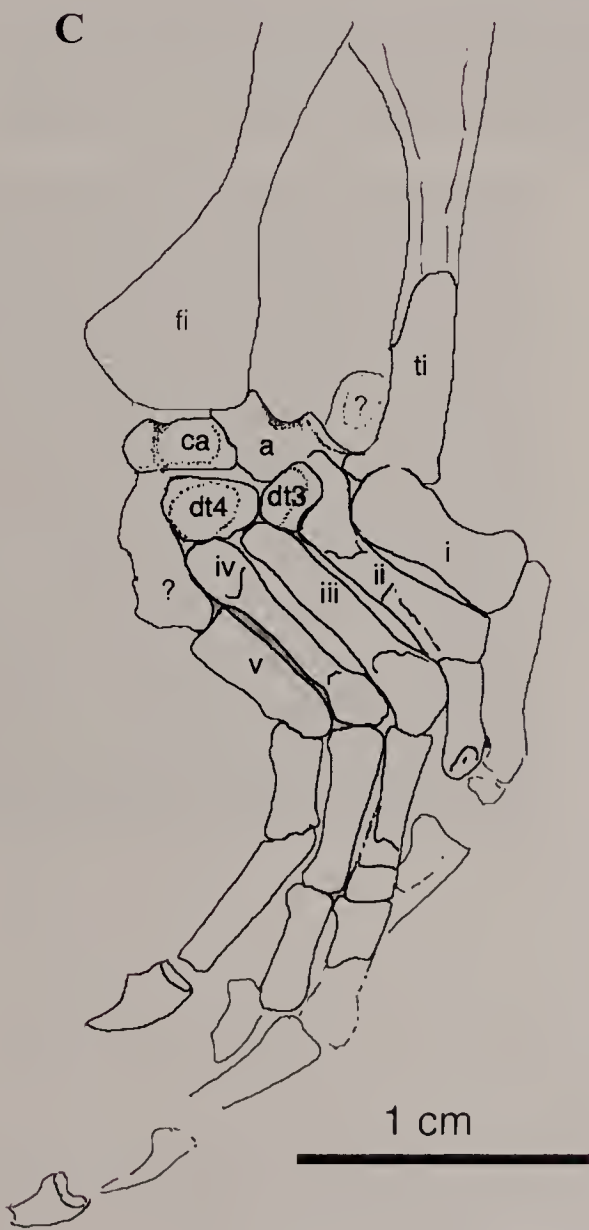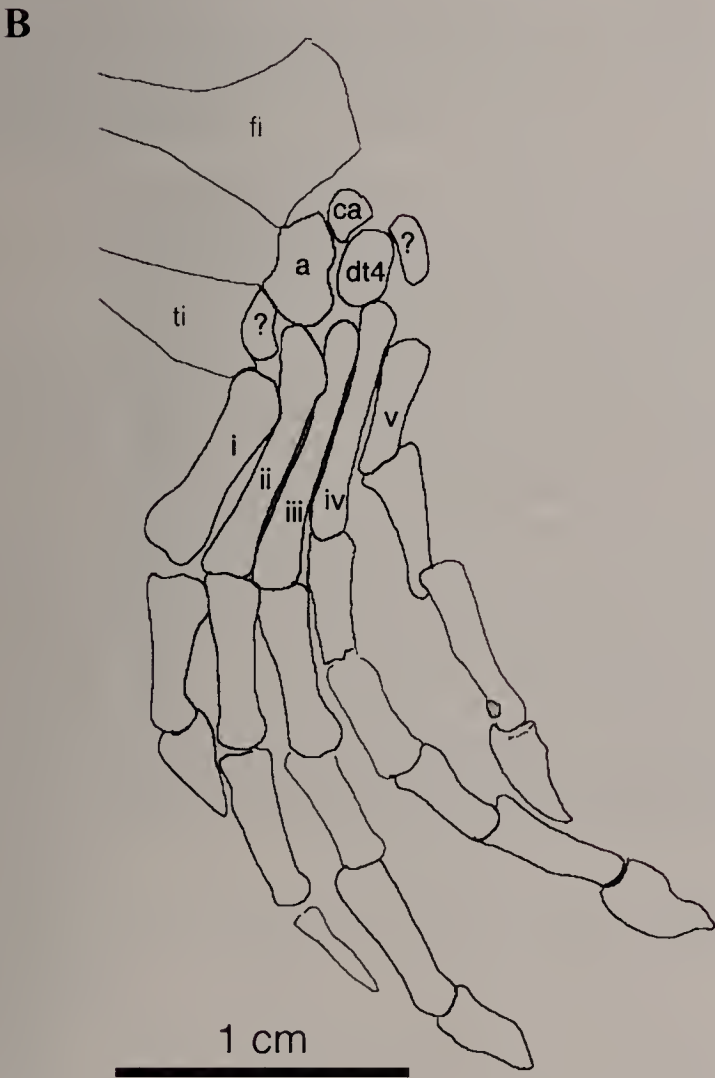
Fig. 12 - Rearlimbs of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of rearlimbs, pelvis, and anterior cauda; B) line drawing of left rearlimb; C) line drawing of right rearlimb. Abbreviations: a, astragalus; ca, calcaneum; dt3, distal tarsal 3; dt4, distal tarsal 4; fi, fibula; ti, tibia; i-v, metatarsals 1 to 5; ?, anterior astragalar ossification.

SQUAMATION AND TRACHEAL RINGS

Caldwell & Dal Sasso (2004) recently described the squamation of *Pontosaurus kornhuberi* and compared it to the scales of a number of extant squamates. In association with the osteological description presented here, I present a summary of Caldwell & Dal Sasso's (2004) descriptions as well as additional details not given by those authors.

Squamation

Most of the scales of MSNM V3662 are preserved as articulated sections of orange to brown permineralized or perhaps carbonized integumentary remnants (Figs. 2, 7, 8, 11-15), while some sections such as those on the cheek, appear to be external casts. Scales range in size from small head scales (1-2 mm) with irregular polygonal outlines (Figs. 2, 13), to regularly organized networks of large diamond-shaped scales on the neck, body, hindlimbs, and tail (Figs. 7, 8, 11, 12, 14, 15); these latter scales appear to be very well imbricated or overlapping.

A number of features separate the various scale regions from each other. The head scales all appear to be non-overlapping structures while all the body scale regions, from the neck to the tip of the tail are imbricated. The transition from non-overlapping to overlapping is abrupt and appears to occur immediately posterior to the presumed location of either an external auditory meatus (Fig. 13 A-C), marked here by the posterior margin of the quadrate. In the cheek to gular region, the gular or neck scales are diamond-shaped while the cheek scales are polygonal and non-overlapping.

The balance of the body margin of MSNM V3662 is well defined by the squamation (Figs. 8, 14, 15). Where preserved, there are large, articulated patches of scales in particular along the posterior half of the specimen and down to the tip of tail (Figs. 1 A-B; 8, 11, 12, 14, 15). In the mid-trunk region, the body margin scales are not well preserved, likely due to preparation of the specimen before the recognition that scales were present. However, in some body regions, for example the tail, the preserved integumentary margins indicate very clearly that the dorsoventral expansion of the tail is twice as deep as the skeletal outline (Figs. 1 B, 8, 15).

The head scales include cheek and jaw scales and possibly a short section of labial scales. Labial scales are located near the jugal and are preserved as a sequence of small, subrectangular scales, each of which bears a tiny protuberance or tubercle at its center (Fig. 13 A, C-D). Cheek and jaw scales vary in size and are elliptical to hexagonal in outline (Fig. 13 A, C-D); these scales compare well with those of the monitor lizard, *Varanus niloticus* but not with those of the Yellow-bellied Sea Snake, *Pelamis platurus* (see Caldwell & Dal Sasso, 2004). Neck scales in MSNM V3662 (Fig. 13 A-B) are small, diamond-shaped, overlapping, and arranged in oblique rows; neck through to tail scales for both *V. niloticus* and *P. platurus* are markedly different (see Caldwell & Dal Sasso, 2004).

The body scales of MSNM V3662 are uniformly sized, diamond-shaped scales that are arranged in oblique rows (Figs. 8, 14, 15). Comparisons to other fossil pythonomorphs with scales show similarities to those of the fossil mosasaur *Tylosaurus proriger* (Snow, 1878) and the fossil aigialosaur *Carsosaurus marchesetti* (Caldwell & Lee, 2001). Comparisons to extant squamates show marked similarities to many terrestrial alethinophidian snakes as well as aquatic alethinophidians such as the Banded Sea Krait, *Laticauda colubrina* (UAMZ 762).

Caudal scale morphology differs from body scale morphology in the hypaxial region of the tail, whereas epaxial caudal scales are comparable in size and organization to the body scales (Figs. 8 C-F, 15 D-E). In MSNM V3662, immediately below the caudal vertebrae, and on top of and below the haemal spines, there are two to three horizontal rows of scales, each of which bears a "keel" (Fig. 15 D-E); the keels on these caudal scales compare well with the keels of the body scales of *Tylosaurus proriger*. Immediately below the keeled tail scales of MSNM V3662 is a single row of tall, overlapping, columnar scales that extend to the ventral margin of the tail. It appears as though these large ventral-most scales (Fig. 15 D-E) were bilaterally paired, though this cannot be positively determined. It is also a possibility, though less likely, that these ventral columnar scales were large, single scales that crossed the ventral caudal midline. The hypaxial caudal scales of MSNM V3662 are similar to those of *Laticauda colubrina* that possesses two or three rows of hexagonal scales (though in *Laticauda* they do not bear a keel), and a single row of bilaterally paired columnar scales that meet at the ventral midline, similar to *Pontosaurus kornhuberi*.

The scales of MSNM V3662 appear to be a blend of the scale types present in extant lizards and snakes. As was discussed by Caldwell & Dal Sasso (2004), small, irregular, non-imbricated head scales associated with small labial scales are observed in iguanids, chamaeleonids, agamids, gekkotans, and varanids, and in acrochordid snakes; in contrast to MSNM V3662, several other squamates, i.e., some iguanids and some snakes (e.g., boas, vipers) combine irregular, non-imbricated head scales with large labial scales. The remaining lizards and most snakes, with the exception of scolecophidians, have large scales on the head and labial margins, which in some are imbricated, but in many are not. The tiny protuberance in the middle of the labial scales appears to be unique to *Pontosaurus*.

Scales on posterior body parts of MSNM V3662 are similar to the imbricated scales of many scincids and iguanids; trunk scales are similar to those of many extant snakes with the exception of scolecophidians and some marine elapids (e.g., *Pelamis platurus*). Interestingly, the amphibious seakrait has scales similar to those of terrestrial snakes, mosasaurs, aigialosaurs, and MSNM V3662. In contrast, body scales of MSNM V3662 are very different from those of extant varanoids such as *Varanus*, *Heloderma*, and *Lanthanotus*.
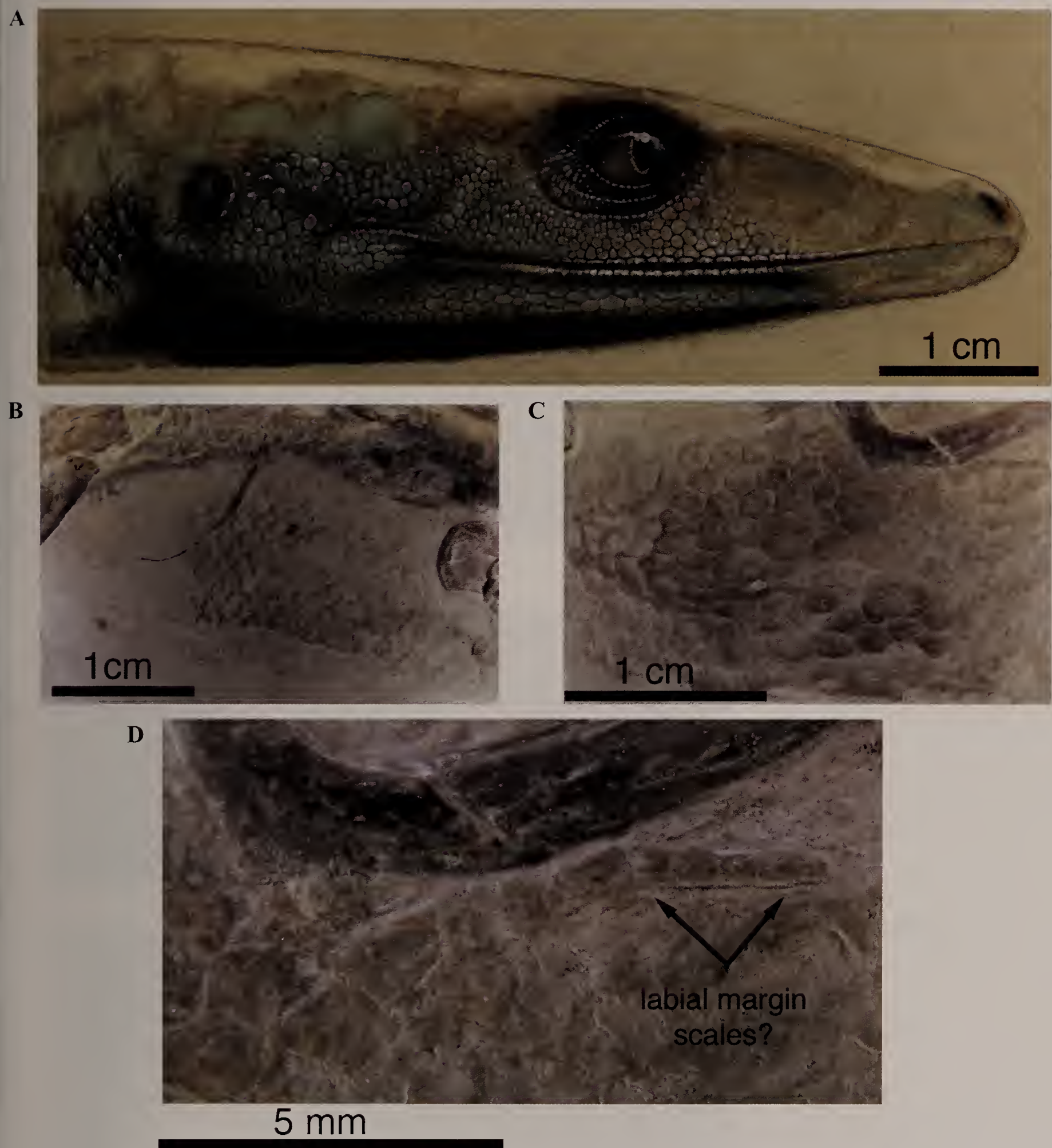
Fig. 13 - Scales on the head and neck region of *Pontosaurus kornhuberi*, MSNM V3662. A) Reconstruction of the head (artist: Fabio Fogliazza); B) detail of neck scales; C) detail of cheek scales; D) detail of lower portion of jugal bar illustrating possible labial scales.
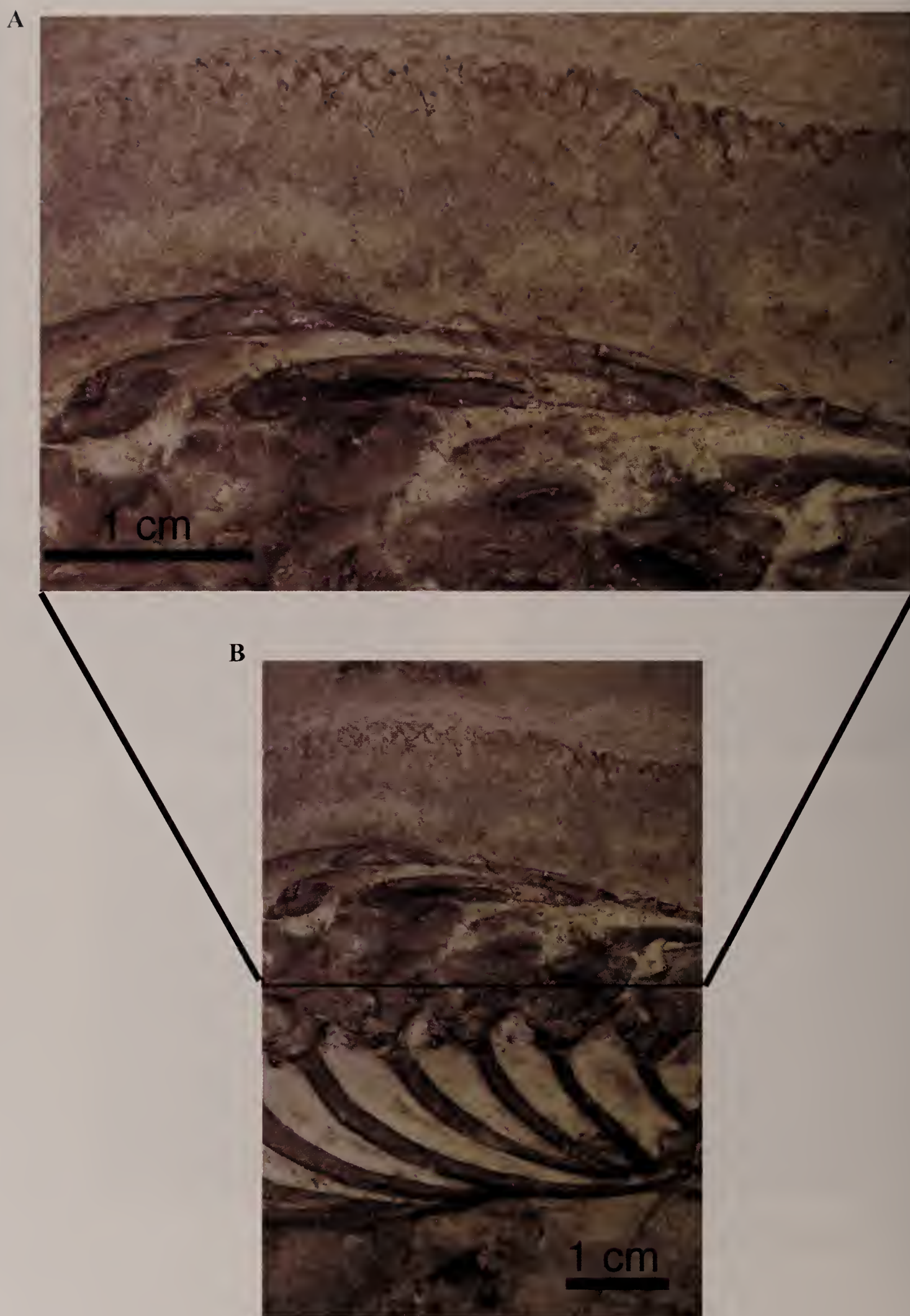
Fig. 14 - Scales on the trunk of *Pontosaurus kornhuberi*, MSNM V3662. A) Detail of scales at mid-trunk, vertebrae 17-21; B) photo of mid-trunk region. 'A' is a magnified portion of the upper part of photo 'B'.
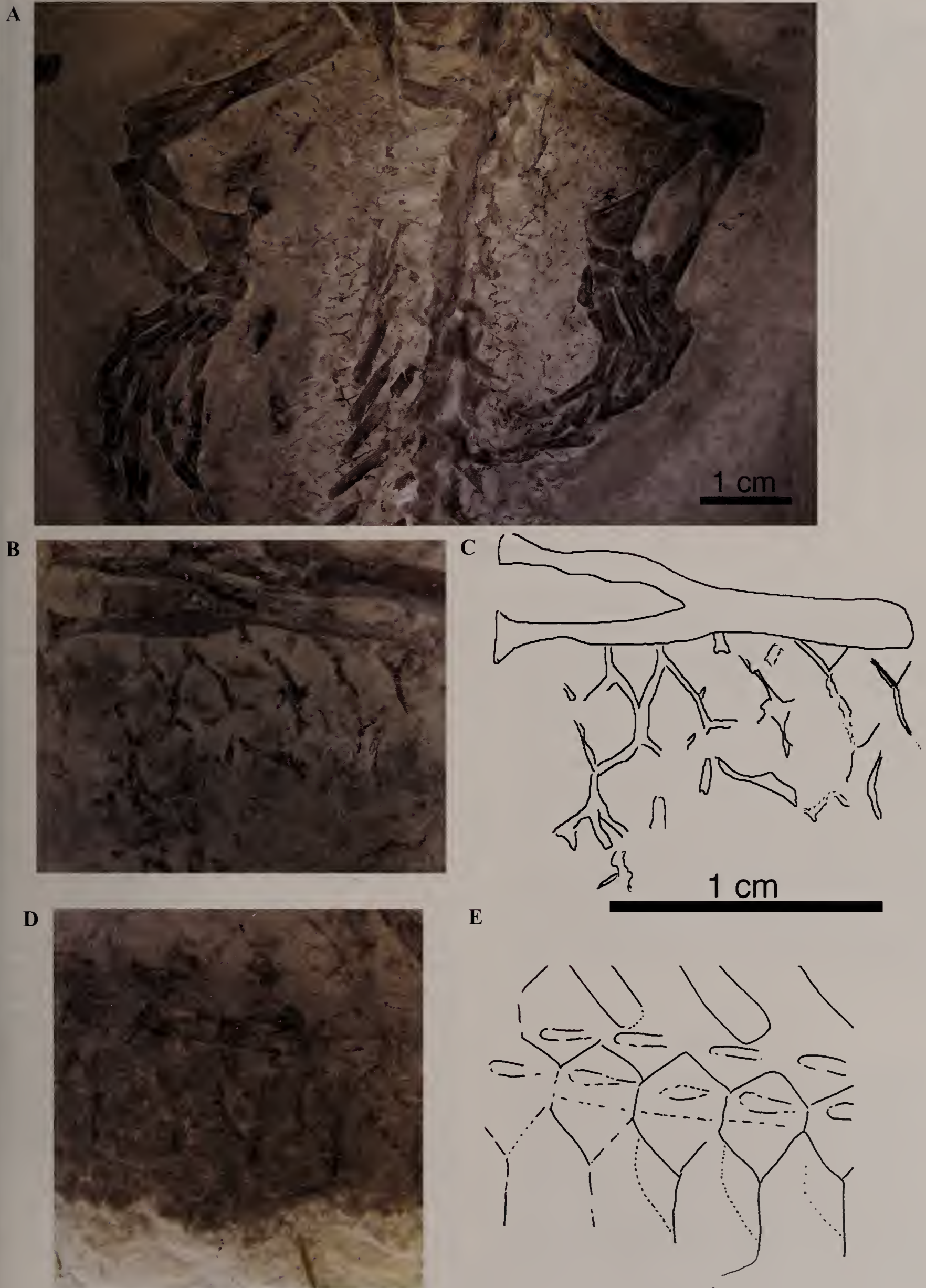
Fig. 15 - Pelvic and caudal scales of *Pontosaurus kornhuberi*, MSNM V3662. A) Overview of rearlimbs, pelvis, and anterior cauda; B) photo detail of anteriormost and ventral caudal scales; C) line drawing of photo 'B'; D) photo detail of midcaudal scales and ventral columnar scales; E) line drawing of photo 'D'.

Tracheal and ?bronchial? rings

The trachea, as represented by the preserved tracheal rings present in the cervical region and the anteriormost portion of the trunk, was naturally long, but also had a rather large diameter (Fig. 16) at approximately 3-4 mm. The preserved tracheal rings are exposed to the right of the axis cervical vertebra (Fig. 7 A-C) and are exposed on the right side of the specimen through to C5 where they disappear under C6-7 reappearing at C8 and crossing the internal surface of the clavicle-interclavicle (though not well preserved here) to reappear between the left side ribs of the first, second and third dorsal vertebrae (Fig. 9). At this point, it is tempting to refer to these rings as preserved portions of the left bronchus since presumably at this point, the trachea had bifurcated into the right and left bronchi. This series of tracheal and perhaps bronchial rings is the best-preserved and most continuous sequence for any known pythonomorph and possibly any lepidosauromorph.

Fig. 16 - Tracheal rings of *Pontosaurus kornhuberi*, MSNM V3662.

PHYLOGENETIC ANALYSIS

Of the squamate synapomorphies recognized by Estes *et al.* (1988), *Pontosaurus kornhuberi* possesses the following: reduced nasals, transverse frontoparietal suture, angular not reaching mandibular condyle, single headed ribs, cervical intercentra form prominent hypapophyses, loss of entepicondylar foramen in humerus, enlarged distal epiphysis of ulna, loss of gastralia, proatlas absent, premaxillae fused, parietal fused, jugal forms anteroventral border of orbit, procoelous vertebrae, dorsal intercentra lost, and an anterior coracoid emargination. As a result, it is accepted *a priori* that it is a squamate, a statement that need not be tested phylogenetically.

Additionally, *Pontosaurus kornhuberi* also possesses the following anguimorph synapomorphies as recognized by Estes *et al.* (1988): cervical intercentra sutured to posterior part of preceding centrum and more than 26 presacral vertebrae.

Methodology

Phylogenetic relationships of *Pontosaurus kornhuberi* and *Pontosaurus lesinensis* were examined by integrating the detailed osteological description presented here into a highly modified version of Pierce & Caldwell's (2004) data matrix (characters and state codings) of pythonomorph squamates (a modified analysis of Lee & Caldwell's [2000] squamate data matrix). A large number of characters were uninformative when balanced against the reduced ingroup used here and so were deleted. Several character states were modified, in particular for *Pontosaurus lesinensis*, and some character descriptions were also modified.

The analysis presented here only includes the ingroup pythonomorphs as identified by Pierce & Caldwell (2004): aigialosaurs and mosasaurs (Lee & Caldwell, 2000), *Pachyrhachis problematicus* (Lee & Caldwell, 1998), *Pachyophis woodwardi* (Lee *et al.*, 1999), *Aphanizocnemus libanensis* (Dal Sasso & Pinna, 1997), the Dolichosauridae [which includes *Dolichosaurus longicollis* and *Coniasaurus crassidens*/*Coniasaurus gracilodens* (Caldwell 1999, 2000; Caldwell & Cooper, 1999)], *Adriosaurus suessi* (Lee & Caldwell, 2000), *Pontosaurus lesinensis* (Pierce & Caldwell, 2004), and *Pontosaurus kornhuberi* (this study). These taxa were coded for 77 osteological characters (Appendix I) modified from the character descriptions listed by Pierce & Caldwell (2004). Cladograms were produced using the Branch-and-Bound algorithm as written into the computer software application PAUP Version 4.0b10 (Swofford, 2002). All characters were analyzed unordered and unweighted; terminal polymorphisms were interpreted as "uncertainty regarding the primitive state" when calculating tree lengths. The modern varanid lizard *Varanus* sp. was coded for these same 77 characters and used as the outgroup taxon for rooting the tree and polarizing character state transformations. The selection of *Varanus* as outgroup in this analysis follows the justifications as given by Tchernov *et al.* (2000) in their analysis of snakes, and the findings of Rieppel & Zaher (2000) regarding varanid-mosasaurid relationships as presented in their critique of Lee (1998).

Results

Cladistic analysis of the data matrix (Appendix II) resulted in 9 equally most-parimonious cladograms with tree lengths of 119 steps, Consistency Indices (C.I.) of 0.773, Homoplasy Indices (H.I.) of 0.226, and a Retention

Indices (R.I.) of 0.727. Aigialosaurs and mosasaurs form a resolved clade in all nine cladograms as do the ophidians, *Adriosaurus* and the two pontosaurs; the Dolichosauridae are consistently reconstructed as the sistergroup to all other non-mosasauroid pythonomorphs (see the Strict Consensus Tree, Fig. 17 A). The unstable taxon is the Lebanese marine lizard, *Aphanizocnemus libanensis*. In three trees it is the sistergroup to all non-mosasauroid pythonomorphs, in three more it forms a clade with the Dolichosauridae, and in the final three it is resolved as the sistergroup to all pontosaurs, *Adriosaurus* and ophidians.
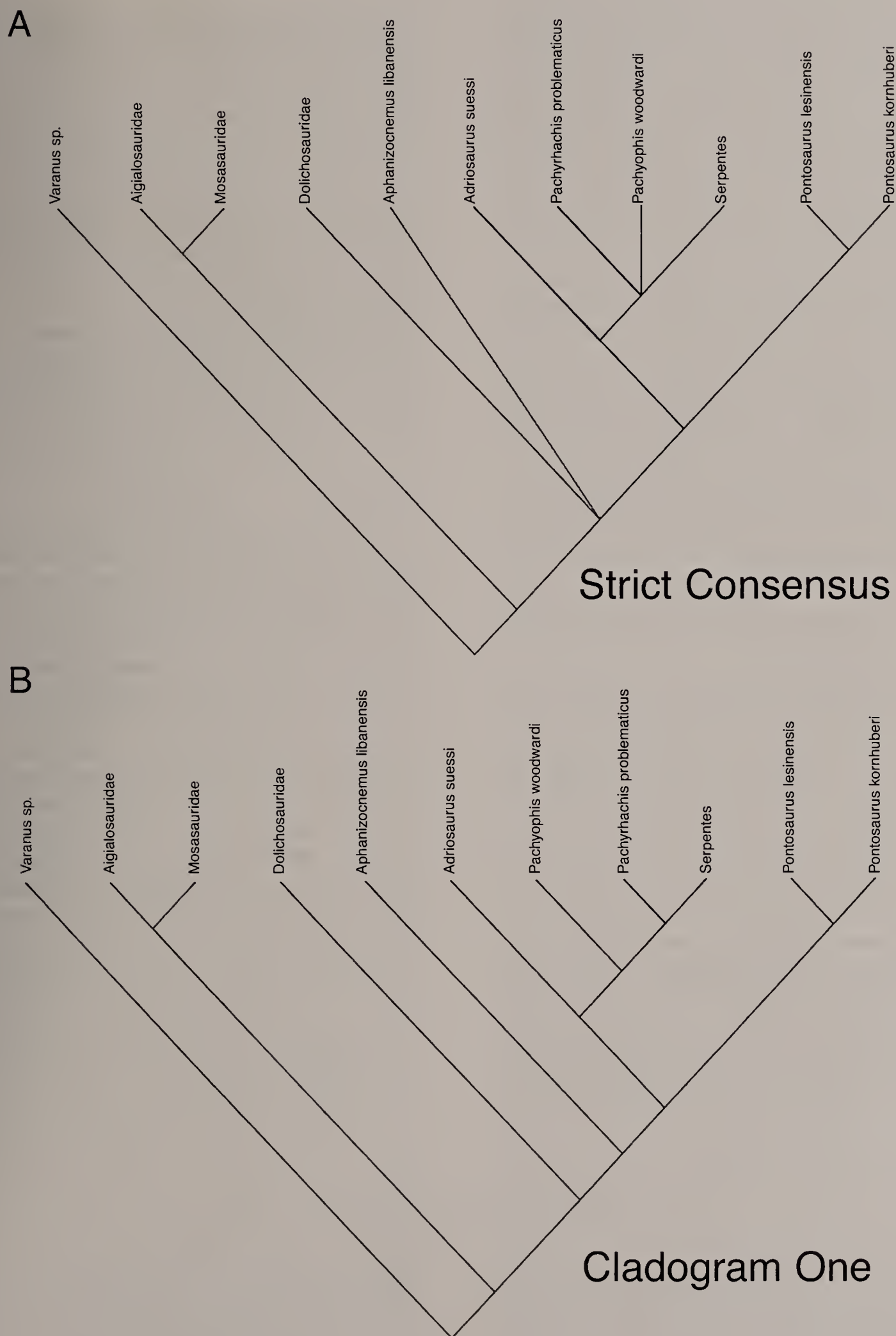
Fig. 17 - A) Strict consensus phylogeny and B) Cladogram Number One, resulting from cladistic analysis of ten pythonomorph squamate taxa using 77 osteological characters. This analysis resulting in nine most parsimonius trees (Tree length, 119 steps; Consistency Index (C.I.= 0.773); Homoplasy Index (H.I. = 0.226); Retention Index (R.I. = 0.727).

Character distributions

The synapomorphies supporting the various clades are the only important components of any phylogenetic statement as derived from a cladogram, or series of cladograms (i.e., a consensus tree interpreted as a phylogeny). As cladograms are constructed by character state distributions, the nature of the characters and states as described, and subjective decisions that were made in their delineation and construction, are the key elements of any phylogenetic hypothesis. Statistical support, other than the information supplied by consistency and homoplasy indices, is not given in this study. From my point of view, a character may well be homoplastically distributed and not at all "robust" on a statistical basis. However, this lack of robustness may stem from at least two alternatives in terms of phylogenetic history or non-history: 1) the taxic sample is incomplete but the character is accurately described; 2) the character is inaccurately described and the taxic sample is incomplete. In either case, because we are testing sistergroup relations, not heuristically recovering ancestors, we must always assume that the taxic sample is incomplete. What is likely impossible to determine is the delineation and character state subdivision of the feature being characterized. No statistical test, administered subsequent to the cladistic parsimony analysis, can determine the phylogenetic value of a character statement. In other words, I do not accept the value of decay indices such as Bremer Support etc., and have not applied such tests to the analysis of character distributions, the characters of which, and their states, are still the object of great scrutiny.

The following review of synapomorphy/apomorphy distributions reflects the character distributions for cladogram number one (Fig. 17 B).

(Aigialosauridae, Mosasauridae) - This clade is supported by six synapomorphies: 6 (0=>1), Jugal extends anteriorly past orbit; 48 (0->1), Coronoid anteromedial margin does not contact splenial; 49 (0=>1), Surangular forms half of articular cotyle (1); 60 (0=>1), Transverse processes of cervicals on middle of centrum; 61 (0=>2), Cervical intercentra (excluding atlas and axis intercentra) not sutured or fused to preceding centrum; 72 (1=>2), Number of rib attachment points to sternum, five pairs.

(*Dolichosauridae*, (*Aphanizocnemus* ((*Pontosaurus lesinensis*, *Pontosaurus kornhuberi*) (*Adriosaurus* (*Pachyophis* (*Pachyrhachis*, Serpentes)))))) - This clade is supported by 17 synapomorphies: 1 (1->0), Premaxillary lateral foramina absent; 20 (0->1), Supratemporal in superficial position, on dorsolateral surface of parietal; 27 (1->2), Decensus parietalis, prominent flanges form sidewall of braincase contacting entire dorsal margin of prootic; 29 (0->1), Optic foramina enclosed partly or entirely by frontals; 30 (0->1), Trigeminal foramen or foramina, anterior margin enclosed by descending flange of parietal; 31 (0->1), Crista prootica (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis) reduced to weak ridge, or absent; 32 (1->0), Basisphenoid without long posterolateral flanges; 33 (0->1), Supraoccipital situated posterior to parietal, forms part of posterior skull roof; 34 (0->1), Post-temporal fenestra completely closed via sutural contact of the skull roof and otic region of braincase; 35 (1->2), Opening of Jacobson's organ enclosed fully by vomer and septomaxilla only, not confluent with choana; 38 (1->0), Palatine as long as vomer; 39 (0->1), Palatine with distinct rectangular process projecting medially from the middle portion of the palatine to the skull midline; 59 (0->1), Number of cervical vertebrae ten to eleven; 66 (0=>1), Scapulocoracoid present but reduced; 69 (0->1), Interclavicle present but reduced; 73 (0=>1), Forelimbs small (1); 76 (0->1), Scleral ossicles thirteen or fewer.

(*Aphanizocnemus* ((*Pontosaurus lesinensis*, *Pontosaurus kornhuberi*) (*Adriosaurus* (*Pachyophis* (*Pachyrhachis*, Serpentes))))) - This clade is supported by 6 synapomorphies: 2 (0->1), Premaxilla-maxilla contact mobile and non-sutural; 12 (0->1), Frontoparietal suture, in dorsal view, complex curved or interdigitating contact; 26 (0->2), Ventromedial processes of frontals contacting parabasisphenoid below olfactory tracts; 42 (0->1), Mental foramina on lateral surface of dentary, two or fewer foramina; 44 (1->0), Subdental shelf weakly developed; 71 (0->1), Ossified sternum absent.

((*Pontosaurus lesinensis*, *Pontosaurus kornhuberi*) ((*Adriosaurus* (*Pachyophis* (*Pachyrhachis*, Serpentes)))) - This clade is supported by 3 synapomorphies: 46 (0->1), Splenial, small, only reaching middle of tooth row (1); 62 (0=>1), Pachyostosis of mid-dorsal vertebrae and ribs, present; 63 (0=>1), ribs, long, not curved, body laterally compressed.

(*Adriosaurus* (*Pachyophis* (*Pachyrhachis*, Serpentes))) - This clade is supported by 17 synapomorphies: 4 (1->0), Posterior process of maxilla long, reaching or extending past middle of ventral margin of orbit; 8 (1->0), Antorbital ridge absent; 9 (0=>1), Frontals, paired elements; 15 (0=>1), Postorbital ventral process prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone; 23 (0->2), Quadrate, distinct tympanic crest absent and external surface of quadrate only weakly concave; 24 (1->0), Quadrate shape without large, posteroventrally curved, suprastapedial process; 28 (0->1), decensus parietalis contacting parabasisphenoid; 36 (0->1), Vomer entirely medial to palatine; 37 (0->1), Palatine-vomer contact mobile, non-sutural contact; 40 (1->0), Interpterygoid vacuity ("pyriform recess" of Estes *et al.*, 1988) open and wide; 44 (0->2), Subdental shelf absent; 45 (1->2), Posterior margin of lateral surface of dentary, deep notch present; 48 (0->1), Coronoid anteromedial margin does not contact splenial; 51 (1->2), Articular fused with prearticular and surangular; 55 (0->1), Palatine teeth present; 68 (0->1), Clavicle absent; 75 (0->1), Scleral ossicles absent.

(*Pachyophis* (*Pachyrhachis*, Serpentes)) - This clade is supported by 14 synapomorphies: 5 (0=>1), Lacrimal absent, never present as a discrete element; 10 (0->1), Frontal excluded from orbital margin, prefrontal contacts postfrontal or postorbital; 17 (0=>1), Pineal foramen absent; 18 (0=>2), Parietal table and jaw adductor muscles, parietal table has a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal; 19 (0=>1), Upper temporal arch incomplete, upper and lower temporal fenestra confluent; 52 (0->1), Retroarticular process size short, < articular cotyle; 57 (0->1), Vertebral articulatory surfaces vertical, condyles (if present) facing

posteriorly, much of the articulatory surface is visible in ventral view; 58 (0=>3), Number of presacral vertebrae 120 or more; 59 (1=>2), Number of cervical vertebrae more than twelve; 64 (0=>1), Distally forked cloacal ribs ("lymphapophyses") present; 66 (1=>2), Scapulocoracoid absent; 73 (1=>2), Forelimbs absent; 74 (1->0), Epipodials parallel; 77 (0=>1), Epiphyses on appendicular skeleton absent.

(***Pontosaurus lesinensis, Pontosaurus kornhuberi***) - This clade is supported by 10 synapomorphies: 3 (1=>0), Dorsal process of maxilla on middle or anterior end of maxilla; 21 (1=>0), Supratemporal small, less than half the maximum width of the skull; 22 (1->0), Quadrate suspension, mobile, articulates dorsally with squamosal, supratemporal and opisthotic; 41 (1->0), Pterygoid, anterior (palatine) process merges gradually, in a gentle curve, with the lateral (ectopterygoid) process; 50 (1->0), Adductor fossa faces dorsomedially; 52 (0=>2), Retroarticular process size long, >2 times articular cotyle; 61 (0=>1), Cervical intercentra (excluding atlas and axis intercentra) sutured to preceding centrum (1); 65 (0->1), very laterally compressed, transverse processes reduced anteriorly, absent posteriorly, chevrons and neural spines elongated; 69 (1->0), interclavicle present.

Discussion

The phylogenetic analysis presented here supports Nopcsa's (1903) claim that *Pontosaurus* is more closely related to other dolichosaurs and snakes than to the aigialosaurs (Kramberger, 1892); the varanoid question debated by Kornhuber (1873) and Kramberger (1892) was not tested here. The phylogenetic position of *Pontosaurus* further reinforces the assertion that dolichosaurs are the sister group to all modern and extinct snakes as recently suggested by Pierce & Caldwell (2004) and Lee & Caldwell (2000), and more historically, by Nopcsa (1908, 1923).

As was argued by Pierce & Caldwell (2004), the analysis presented here also supports the idea that the family Dolichosauridae is a paraphyletic assemblage as indicated by the following sistergroup structure from Cladogram 1 [(*Dolichosaurus*, (*Aphanizocnemus* ((*Pontosaurus lesinensis, Pontosaurus kornhuberi*) (*Adriosaurus* (*Pachyophis (Pachyrhachis,* Serpentes))))))] (Fig. 17 B).

It should be noted however, that the paraphyly of Nopcsa's Dolichosauridae, inclusive of "dolichosaurs" other than *Dolichosaurus* and *Coniasaurus*, could be a consequence of the taxa and/or characters used in this analysis; alternatively, if arguments presented by Rieppel & Zaher (2000) are ever tested by original analysis then it is possible the topology hypothesized here will be found to be polyphyletic and that the Dolichosauridae is in fact a monophyletic assemblage exclusive of snakes. As noted, Rieppel & Zaher's (2000) contention has not yet been corroborated by the presentation of a testable hypothesis.

In terms of the selection of taxa and characters, it is important to point out that there are nine known species of non-mosasaurid and non-aigialosaur Cenomanian-aged marine squamates that are referred to as "dolichosaurs"; however, only five were incorporated into the above analysis. A detailed re-examination of all known dolichosaurs, such as *Acteosaurus tommasinii* (Meyer, 1860) and *Eidolosaurus trauthi* (Nopcsa, 1923), is necessary in order to complete the data set.

For example, recent re-assessment of *Acteosaurus crassicostatus* by Caldwell & Lee (2004) indicated that the taxon is not diagnosable and that the specimens assigned to the species by Calligaris (1993) are diagnosable as *Adriosaurus suessi*. Attempts to code *E. trauthi* resulted in only 18% of the 159 characters being coded; the characters and the taxon were removed from the final matrix due to the inordinately high amount of missing data.

What is ultimately needed is a detailed examination and test of the monophyly of the Pythonomorpha (mosasaurs, aigialosaurs, dolichosaur, pontosaurs, adriosaurs, acteosaurs, and snakes). Rieppel & Zaher (2000) recently re-examined and criticized Lee's (1998) character evidence as used in support of the hypothesis of a monophyletic Pythonomorpha. Their analysis found pythonomorphs to be non-monophyletic, with the Mosasauroidea nested within varanoids and snakes nested with a clade including amphisbaenids and dibamids; all of these squamates were found to be anguimorphs. Although Rieppel & Zaher (2000) used the results of their analysis to reject Lee's (1998) assertion of a monophyletic Pythonomorpha, they did not accept their own phylogenetic tree as an accurate representation of squamate relationships; this makes their "falsification" unacceptable. A critical review of the character codings used in this study and those employed by Rieppel & Zaher (2000) along with an additional analysis including all known pythonomorphs is necessary to resolve the monophyly of the Pythonomorpha. A rigorous analysis of mosasaurs, aigialosaurs, dolichosaurs, pachyophiids, and snakes might alter both our understanding of pythonomorph phylogeny and by extension snake origins.

FUNCTIONAL MORPHOLOGY

Aquatic environments present very specific physical and environmental constraints on the successful adaptation and evolution of the inhabitant organisms. For secondarily aquatic tetrapods the parameters of these constraints influence anatomies related to buoyancy control, respiration, locomotion, vision, hearing, chemosensory perception, feeding, and reproduction (Pl. 1).

For example, extinct aquatic squamates responded to these constraints and the selection pressures imposed by them, through the evolution of pachyostosis in the ribs and vertebrae in order to solve problems of buoyancy. In some groups, such as dolichosaurs, they evolved elongate necks and snouts to address the constraints of ambush feeding underwater. Mosasaurs solved locomotory problems in a

viscous fluid via modifications to the axial skeleton to support carangiform locomotion, and by modifying the limbs into hydrofoils/paddles by shortening the upper and lower limb, and lengthening and broadening the hand and foot.

Similar evolutionary solutions to these physical and environmental constraints are preserved in the fossilized skeletons of early aquatic snakes (Caldwell & Lee, 1997; Rage & Escuillié, 2000; Tchernov *et al.*, 2000; Rieppel & Head, 2005), dolichosaurs (Caldwell, 1999, 2000; Caldwell & Cooper, 1999; Lee & Caldwell, 2000) (e.g., MSNM V3662), aigialosaurs (DeBraga & Carroll, 1993; Caldwell & Lee, 2001), and in particular, the giant marine mosasaurs (Russell, 1967; Bell, 1997).

Pontosaurus

The anatomy and morphology of the complete tail of *Pontosaurus kornhuberi*, as exemplified by MSNM V3662, with 163 vertebrae comprising 68% of the total body length (TBL), suggests that this structure was the primary propulsive organ for aquatic locomotion (Fig. 18 A). Because pontosaurs and dolichosaurs are among the earliest known aquatically adapted lizards (Kornhuber, 1873; Pierce & Caldwell, 2004) along with pachyophiid snakes (Lee & Caldwell, 1998), and have been hypothesized to be the sister-group to snakes (Lee & Caldwell, 2000), the adaptations of pontosaurs and dolichosaurs provide important insights into aquatic evolution and adaptation in early marine squamates.

A useful comparison of body proportions gives some insight into the functional morphology of *Pontosaurus*. Caldwell & Dal Sasso (2004) compared *Pontosaurus kornhuberi* to two modern, aquatic squamates, the Galapagos Marine Iguana and the Yellow-bellied Sea Snake (Fig. 18 A-C). Those authors showed that the tail of *Pontosaurus* is proportionately longer, and is dorsoventrally deepened along most of its length as compared to either a sea snake or the marine iguana. This is an important distinction as it indicates that seasnakes locomote not with their tail (carangiform locomotion) but with their entire bodies (anguilliform locomotion); by comparison, the marine iguana, which swims in a carangiform-sub-carangiform mode, does so with a proportionately shorter tail. Another level of comparison can be made between pontosaurs and mosasaurs in the percent total body length (TBL) of the tail, which ranges between 30% and 48% in the latter (Russell, 1967). In other words, pontosaurs had very short bodies, long necks, and extremely long tails as compared to the more derived mosasaurs, to their sister group, the snakes, and to the modern marine iguana.

Comparing the osteology of the tail of a marine iguana with the tail of *Pontosaurus kornhuberi*, it is evident that the latter is much more laterally compressed; comparison with the sea snake indicates a similar degree of compression to pontosaurs. The anterior-most haemal arches and transverse processes of MSNM V3662 present a broad and deepened set of surfaces for the insertion of a large and powerful caudofemoralis musculature (lateral to the hypaxially oriented anterior haemals immediately posterior to the reduced ischium) that would have been used to "drive" the movements of the tail. The adaptive importance of the tail as the aquatic locomotory organ for Cretaceous marine squamates cannot be overemphasized; even in later groups of marine lizards such as mosasaurs, which evolved paddle-like limbs, the primary locomotory organ was clearly the tail. A brief examination of caudal osteology in mosasaurs highlights a number of features shared with *Pontosaurus kornhuberi*, but also reveals the presence of a large and variable number of pygal vertebrae (i.e., caudals without haemal arches).

The transverse processes of the two pygal vertebrae are very large and would have served as an enormous and very long series of attachment sites for the caudofemoralis musculature (ranging from 15-50% of total tail length). Additionally, the long pontosaur tail would have been essential to tail-driven locomotion since the body was likely made more rigid by the high degree of pachyostosis. This rigidity may have decreased the severity of lung compression, allowing limited respiration during powerful surface locomotion.

A second feature of the axial skeleton of *Pontosaurus kornhuberi* that is likely related to tail driven locomotion is the anatomy of the ilium (Fig. 11), specifically the iliac crests. In *P. kornhuberi* the only crest and process that is well developed is the posterior superior iliac crest, thus giving a broad proximal attachment surface for the femoral flexors. There is no anterior extension of the ilium that would serve as the proximal attachment site for the femoral extenders. The overdevelopment of the posterior attachment sites, as compared to the underdevelopment of the extensor attachments, may well represent a functional focus on the limb flexor musculature synergistically associated with the flexion of the caudofemoralis. Contractile flexion of the caudofemoralis musculature would adduct the femora towards lateral surface of the tail. Synergistic flexion of the femur and tibia, by contraction of the femoral and tibial adductor musculature proximally attached to the posterior iliac crest (*e.g., adductor femoris, flexor tibialis internus and externus*), may well have contributed to the caudal powerstroke driven by contraction of the *caudofemoralis*. Retraction of the femur would have been largely passive thus re-building elastic kinetic energy into the muscles of the opposite and stretched muscles fibers prior to the next contraction. This anatomy also suggests that the synergistic powerstroke was rapid, strong and provided a burst of speed, pursuits designed for ambush style predation.

Building on this functional model, the anatomy of the pubis and ischium present a broad contact along the ventral aspect of midline of the body. This morphology indicates that the *puboischiofemoralis* and *puboischiotibialis* were all well-developed in their proximal attachments. These muscles serve to pull the lower limb towards the midline of the body, again, likely in synergy with the *caudofemoralis*; again, retraction of the femur and tibia would be passive and occurring in opposing waves, right to left.

For slow swimming, it seems reasonable to model gentle caudal driven locomotion with the limbs held tightly against the body. For high speed sudden power bursts, the functional model suggested here would likely involve

strong contractions, in opposite waves, where the limbs were strongly adducted and retracted, adducted and retracted in a right-left pattern.

Following on the use of the rearlimbs in the sudden burst, tail driven locomotion, is the aspect of that limb and how it would have interacted with the water. Both the front and rear limbs are extremely reduced in size in *Pontosaurus kornhuberi*; additionally, the forelimb shows negative allometric growth in relation to the rearlimb. Some of this size difference can be attributed to the anatomy and inferred function of the rearlimb musculature in locomotion as discussed previously. However, despite the size and functional difference between the two limbs, they are similar to each other in terms of their degree of flattening in the lower limb region, the width of the antebrachium, and the elongation and flattening of the manus/pes (Figs. 10, 12). As discussed previously, this flattening and the widening of the limb likely prevented pronation of the forelimb via rotation of the radius. This would effectively have limited the ability of *P. kornhuberi* to locomote efficiently in terrestrial environments using its limbs; there is no indication that this animal could not have propelled itself effectively using axial locomotion, similar to a modern legless lizard (e.g., *Ophisaurus apodus*) or a seakrait (e.g., *Laticauda colubrina*). Similarities of body morphology and proportion link legless lizards and *P. kornhuberi* while the ventral scales of *P. kornhuberi* are similar to those of sea kraits (Caldwell & Dal Sasso, 2004) which also are able to move about on land, unlike true sea snakes.

The other feature of limb morphology in *Pontosaurus kornhuberi* that is important to consider, is the hydrofoil potential of a broad and flattened lower limb and manus/pes. This is particularly important for the rearlimb as functionally reconstructed in the caudal powerstroke. If the limb was passively retracted due to muscle fiber stretching in response to total fiber recruitment during powerful contractions, then it would have been efficient as a hydrofoil if it presented a low hydrofoil aspect preaxially to postaxially. The widening of the antebrachium and flattening of the elements supports this functional model for the rearlimb.

As a result of its small limbs, more rigid trunk, and extremely long tail, it seems likely that *Pontosaurus kornhuberi* had reduced potential for terrestrial locomotion but was likely an excellent swimmer, employing its unique anatomies to problems of aquatic locomotion. It possessed at least several rows of caudal scales that may have assisted in reducing drag; later groups such as mosasaurs appear to have covered the entire body with keeled scales. Pontosaurs also evolved incredibly long tails that were laterally very compressed and thus presented a high surface area for power strokes during lateral undulatory locomotion. Finally, the anterior-most caudals show an osteology that is very suggestive of the presence of large caudofemoralis muscles (a small number of pygals and the presence of large transverse processes); these muscles are critical to tail-driven locomotion and became very important in the later, and very successful, giant mosasaurs.
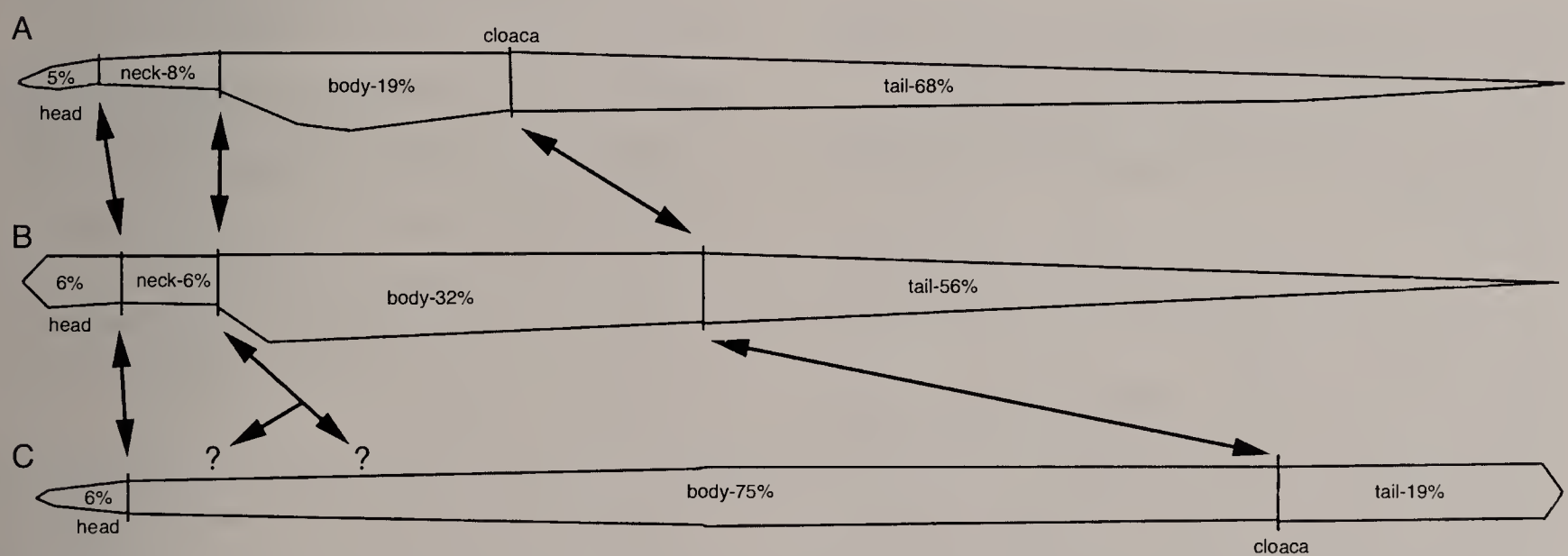
Fig. 18 - Body proportions of fossil and extant marine squamates. A) *Pontosaurus kornhuberi*, MSNMV3662; B) *Amblyrhynchus cristatus*, modern Galapagos Marine Iguana; C) *Pelamis platurus*, modern Yellow-bellied Sea Snake.

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A new species of *Pontosaurus* (Squamata, Pythonomorpha) from the Upper Cretaceous of Lebanon and a phylogenetic analysis of Pythonomorpha
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APPENDIX I

Character List

(a) skull roof

1. Premaxillary lateral foramina. Absent (0); present (1).
2. Premaxilla-maxilla contact. Immobile and sutural (0); mobile and non-sutural (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (0) to state (1).
3. Dorsal process of maxilla. On middle or anterior end of maxilla (0); on posterior half of maxilla (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (1) to state (0).
4. Posterior process of maxilla. Long, reaching or extending past middle of ventral margin of orbit (0); short, not reaching middle of ventral margin of orbit (1).
5. Lacrimal. Present, either permanently separate or fusing with prefrontal during ontogeny (0); absent, never present as a discrete element (1).
6. Jugal. Does not extend anteriorly past orbit (0); extends anteriorly past orbit (1).
7. Nasals. Paired elements (0); single median element (1).
8. Antorbital ridge. Absent (0); present, extending anteriorly from dorsal margin of orbit (1).
9. Frontals. Single median element (0); paired elements (1).
10. Frontal. Enters orbital margin, prefrontal does not contact postfrontal or postorbital (0); excluded from orbital margin, prefrontal contacts postfrontal or postorbital (1).
11. Frontals. Lateral orbital margin deeply concave (0); lateral orbital margin straight or only very slightly concave (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (1) to state (0).
12. Frontoparietal suture. In dorsal view, simple straight transverse contact (0); in dorsal view, complex curved or interdigitating contact (1).
13. Palpebral (superciliary) ossifications on dorsal margin of orbit. Present (0); absent (1).
14. Postorbital. Present (0), absent (1).
15. Postorbital ventral process. Small, forming less than half of posterior orbital margin, postorbital primarily a temporal bone (0); prominent, forming half or more of posterior orbital margin, postorbital primarily an orbital bone (1). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (1) to state (0).
16. Posterior margin of orbit. Present and continuous (0); present but with small gap (1); very incomplete, less than 50% of posterior orbital margin bordered by bone (2).
17. Pineal foramen. Present (0); absent (1).
18. Parietal table and jaw adductor muscles. Parietal table moderately wide, jaw adductors extend onto lateral margin only of dorsal surface of parietal (0); parietal table very wide, jaw adductors restricted entirely to ventral surface of parietal (1); parietal table a narrow sagittal crest, jaw adductors extend over entire dorsal surface of parietal (2). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (2) to state (0).
19. Upper temporal arch. Complete, upper and lower temporal fenestrae separated (0); incomplete, upper and lower temporal fenestra confluent (1).
20. Supratemporal. In deep position, on ventrolateral surface of parietal (0); in superficial position, on dorsolateral surface of parietal (1).
21. Supratemporal. Small, less than half the maximum width of the skull (0); large, at least half the maximum width of the skull (1).
22. Quadrate suspension. Mobile, articulates dorsally with squamosal, supratemporal and opisthotic (0); mobile, articulates dorsally with supratemporal, little or no contribution from other elements (1); mobile, articulates dorsally with opisthotic, little or no contribution from other elements (2). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (?) to state (0).
23. Quadrate. Tympanic crest (outer conch) directed laterally and a well-developed wall (0); tympanic crest directed laterally but a low ridge (1); distinct tympanic crest absent and external surface of quadrate only weakly concave (2).
24. Quadrate shape. Without large, posteroventrally curved, suprastapedial process (0); with large, posteroventrally curved, suprastapedial process (1).
25. Mandibular articulation of quadrate. Saddle-shaped, with lateral and medial condyles (0); flat, a single continuous condyle (1).

(b) braincase and associated structures

26. Ventromedial processes of frontals. Not contacting anything below olfactory tracts (0); abutting or sutured with each other below olfactory tracts (1); contacting parabasisphenoid below olfactory tracts (2).
27. Decensus parietalis. Weakly developed ridges/flanges on ventral surface of parietal (0); prominent flanges descending from lateral margins of dorsum of parietal (1); prominent flanges form sidewall of braincase contacting entire dorsal margin of prootic (2). The coding for *Pontosaurus lesinensis* as given by Pierce & Caldwell (2004) was recoded from state (0) to state (1).
28. Decensus parietalis. Not contacting parabasisphenoid or orbitosphenoid (0); contacting parabasisphenoid (1).
29. Optic foramina. Not enclosed in bone (0); enclosed partly or entirely by frontals (1).
30. Trigeminal foramen or foramina. Anterior margin not enclosed in bone (0); anterior margin enclosed by descending flange of parietal (1).
31. Crista prootica (ridge on lateral surface of the prootic, overhanging foramen pro nervi facialis). Well-developed lateral flange (0); reduced to weak ridge, or absent (1).
32. Basisphenoid. Without long posterolateral flanges (0); with long posterolateral flanges (1).
33. Supraoccipital. Situated ventral or posteroventral to parietal, does not form part of posterior skull roof (0); situated posterior to parietal, forms part of posterior

skull roof (1).

34. Posttemporal fenestra. Present as an opening (0); completely closed via sutural contact of the skull roof and otic region of braincase (1).

(c) palate and associated structures

35. Opening of Jacobson's organ. Enclosed fully by maxilla and vomer, sometimes with a tiny contribution from the septomaxilla, not confluent with choana (0); enclosed partly by maxilla and vomer, confluent posteriorly with choana (1); enclosed fully by vomer and septomaxilla only, not confluent with choana (2).
36. Vomer. Anterior or anteromedial to palatine (0); entirely medial to palatine (1).
37. Palatine-vomer contact. Immobile, sutural contact (0); mobile, non-sutural contact (1).
38. Palatine. Long - as long as vomer (0); short - half as long as vomer (1).
39. Palatine. Without distinct medially-directed process (0); with distinct rectangular process projecting medially from the middle portion of the palatine to the skull midline (1).
40. Interpterygoid vacuity ("pyriform recess" of Estes *et al.*, 1988). Open and wide (0); open and narrow (1).
41. Pterygoid. Anterior (palatine) process merges gradually, in a gentle curve, with the lateral (ectopterygoid) process (0); anterior process distinctly set off from lateral process, the two portions meeting at a distinct "corner" (1).

(d) lower jaw

42. Mental foramina on lateral surface of dentary. Three or more foramina (0); two or fewer foramina (1).
43. Dentary. Curved in lateral view, with concave dorsal (alveolar) edge (0); straight in lateral view, with straight dorsal edge (1).
44. Subdental shelf. Weakly developed (0); large (1); absent (2).
45. Posterior margin of lateral surface of dentary. Shallow notch present (0); no notch present (1); deep notch present (2).
46. Splenial. Large, extending anteriorly past middle of tooth row (0); small, only reaching middle of tooth row (1).
47. Splenial-angular contact. Not, or very slightly, exposed in lateral view (0); greatly exposed in lateral view (1).
48. Coronoid. Anteromedial margin contacts splenial (0); anteromedial margin does not contact splenial (1).
49. Surangular. Does not form large portion of articular cotyle (0); forms half of articular cotyle (1).
50. Adductor fossa. Faces dorsomedially (0); faces dorsally (1).
51. Articular. Separate from both prearticular and surangular (0); fused with prearticular but not surangular (1); fused with prearticular and surangular (2).
52. Retroarticular process size. Intermediate, between 1 and 2 times articular cotyle (0); short, < articular cotyle (1); long, >2 times articular cotyle (2).

(e) dentition

53. Maxillary teeth. Thirteen or more tooth positions (0); between twelve and nine tooth positions (1); eight or fewer tooth positions (2).
54. Dentary teeth. Thirteen or more tooth positions (0); twelve to nine tooth positions (1); eight or fewer tooth positions (2).
55. Palatine teeth. Absent (0); present (1).
56. Pterygoid teeth. Present (0); absent (1).

(f) axial skeleton

57. Vertebral articulatory surfaces. Slightly anterodorsal, condyles facing slightly dorsally, only the ventral edge of the articulatory surface is visible in ventral view (0); vertical, condyles (if present) facing posteriorly, much of the articulatory surface is visible in ventral view (1); anterodorsal, condyles facing very dorsally, none of the articulatory surface is visible in ventral view (2).
58. Number of presacral vertebrae. 27 to 50 (0); 50 to 119 (1); 23 to 25 (2); 120 or more (3).
59. Number of cervical vertebrae. Seven (0); ten to eleven (1); more than twelve (2).
60. Transverse processes of cervicals. On anterior end of centrum (0); on middle of centrum (1).
61. Cervical intercentra (excluding atlas and axis intercentra). Fused to preceding centrum (0); sutured to preceding centrum (1); not sutured or fused to preceding centrum (2).
62. Pachyostosis of mid-dorsal vertebrae and ribs. Absent (0); present (1).
63. Body shape. Round, ribs smoothly curved (0); laterally compressed, middle and distal regions of ribs totally straight (1).
64. Distally forked cloacal ribs ("lymphapophyses"). Absent (0); present (1).
65. Tail. Cylindrical or only slightly lateral compressed, transverse processes well-developed, chevrons and neural spines not elongated (0); very laterally compressed, transverse processes reduced anteriorly and absent posteriorly, chevrons and neural spines elongated (1).

(g) shoulder girdle and forelimb

66. Scapulocoracoid. Present and large (0); present but reduced (1); absent (2).
67. Anterior (primary) coracoid emargination. Present (0); absent (1).
68. Clavicle. Present (0); absent (1).
69. Interclavicle. Present (0); absent (1).
70. Interclavicle. Cross-shaped, with lateral processes (0); simple rod, without lateral processes (1).
71. Ossified sternum. Present (0); absent (1).
72. Number of rib attachment points to sternum. Four pairs (0); three pairs (1); five pairs (2); two pairs or fewer (3).
73. Forelimbs. Large (0); small (1); absent (2).
74. Epipodials. Parallel (0); distally diverging (1).

(h) pelvic girdle and hindlimb

75. Scleral ossicles. Present (0); absent (1).
76. Scleral ossicles. Fourteen (0); thirteen or fewer (1); fifteen or more (2).
77. Epiphyses on appendicular skeleton. Present (0); absent (1).

APPENDIX II

Character Matrix

Taxon	1–30
Varanus sp.	1 0 1 1 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 0 1 0 1 0 0 1 0 0 0 0
Aigialosauridae	? 0 1 1 0 1 ? 1 0 & 0 & ? ? 0 0 0 0 0 0 1 ? 0 1 1 ? 1 ? 0 ?
Mosasauridae	1 0 1 1 0 1 0 1 0 0 1 & & 0 0 0 0 0 0 0 1 1 0 1 1 0 1 0 0 0
Dolichosauridae	? 0 1 1 ? ? ? ? 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ?
Aphanizocnemus libanensi	? ? ? ? ? ? ? ? 0 0 0 ? ? ? ? ? 0 1 ? ? ? ? ? ? ? ? ? ? ? ?
Adriosaurus suessi	? 1 1 & 0 ? ? 0 1 0 0 & 1 ? 1 ? 0 0 0 1 1 ? ? ? ? ? ? ? ? ?
Pachyrhachis problematic	? 1 1 0 1 0 ? 0 1 1 - 1 1 0 1 0 1 2 1 1 1 1 2 0 ? ? 2 1 1 1
Pachyophis woodwardi	? ?
Serpentes	& 1 0 & 1 - & 0 1 & & 1 1 & 1 & 1 2 1 1 & & & 0 & 2 2 1 1 1
Pontosaurus lesinensis	0 1 0 1 ? 0 0 1 0 0 0 0 1 0 0 ? 0 0 0 1 0 0 0 1 1 ? ? ? ? ?
Pontosaurus kornhuberi	0 1 0 1 ? 1 ? 1 0 0 0 1 1 1 0 0 0 0 0 1 0 0 0 1 1 ? 2 0 ? ?

Taxon	31–60
Varanus sp.	0 1 0 0 0 0 0 1 0 0 0 0 0 2 0 0 0 0 0 0 0 0 1 1 0 1 2 0 0 0
Aigialosauridae	? ? ? 0 ? ? ? ? ? ? ? 0 1 1 1 0 1 ? 1 1 1 0 0 0 ? ? 0 0 0 1
Mosasauridae	0 1 0 0 1 0 0 1 0 1 1 0 1 1 1 0 1 1 1 1 1 0 0 0 0 0 & 0 0 1
Dolichosauridae	? ? ? ? ? ? ? ? ? ? ? 0 1 1 1 ? ? 0 ? ? ? ? 0 0 ? ? 0 & 2 0
Aphanizocnemus libanensi	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? 0 ? ? ? ? ? 0 1 0
Adriosaurus suessi	? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? 0 & ? ? ? 0 0 1 0
Pachyrhachis problematic	? ? 1 1 2 1 1 0 1 0 ? 1 1 2 2 0 ? 1 - 1 2 1 0 0 1 0 1 3 2 0
Pachyophis woodwardi	? ? ? ? ? ? ? ? ? ? ? ? 1 2 ? ? 1 ? ? ? ? ? ? 0 ? ? ? 3 2 0
Serpentes	1 0 1 1 2 1 1 & 1 0 1 1 & 2 2 1 & 1 - 1 2 & & & & & & 3 2 0
Pontosaurus lesinensis	? 0 1 ? ? ? ? ? ? 1 0 1 1 0 1 1 1 0 0 0 1 2 0 0 0 1 ? 0 1 0
Pontosaurus kornhuberi	? ? 1 ? ? 0 0 ? ? ? ? 0 1 ? 1 ? ? ? 0 ? ? 2 ? ? ? ? ? 0 1 ?

Taxon	61–77
Varanus sp.	0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 2 0
Aigialosauridae	2 0 0 0 1 0 1 0 0 0 0 2 0 1 ? ? 0
Mosasauridae	2 0 0 0 1 0 & 0 0 1 0 2 0 1 0 0 1
Dolichosauridae	0 0 0 0 ? 1 1 ? 1 ? 0 ? 1 ? ? ? 0
Aphanizocnemus libanensi	2 0 0 0 1 1 0 0 ? ? ? ? 1 ? ? ? ?
Adriosaurus suessi	? 1 1 0 1 1 ? ? ? ? ? ? 1 1 ? ? 0
Pachyrhachis problematic	0 1 1 1 1 2 - 1 1 - 1 - 2 0 1 - 1
Pachyophis woodwardi	? 1 1 ? 1 2 - 1 1 - 1 - 2 ? ? ? ?
Serpentes	0 0 0 1 0 2 - 1 1 - 1 - 2 - 1 - 1
Pontosaurus lesinensis	1 1 1 ? ? 1 1 ? 0 ? 1 ? 1 1 ? ? 0
Pontosaurus kornhuberi	1 1 1 0 0 1 1 0 0 0 0 1 1 1 0 1 0

Pl. 1 - Reconstruction of *Pontosaurus kornhuberi*. Painting by Fabio Fogliazza.

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